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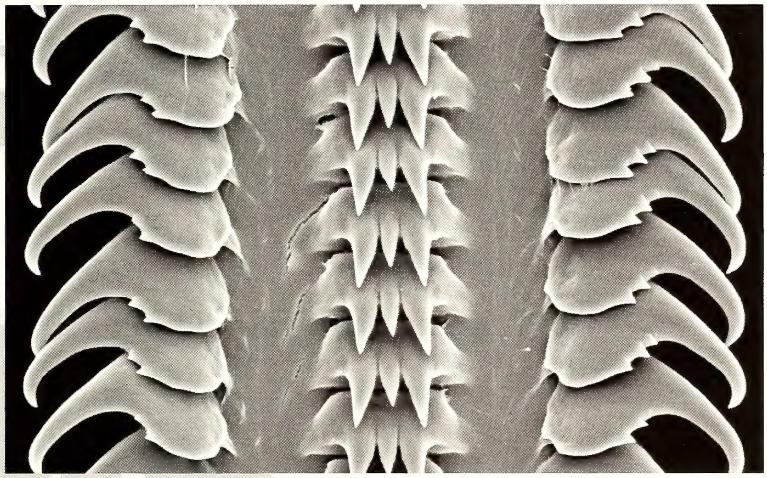

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Cover photo: Radula of *Belloliva simplex* from Kantor & Bouchet

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IN MEMORIAM

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A MESSAGE FROM THE EDITOR

Dear readers,

With the publication of this volume, my term as editor-in-chief of the *American Malacological Bulletin* comes to an end. I would like to thank all of the authors and reviewers who have contributed their work. I am grateful for their patience and cooperation. I feel especially fortunate to have worked with Ángel Valdés of the Natural History Museum of Los Angeles County, who has served as managing editor for the past five years. He is responsible for the new cover and design of the *Bulletin* and has performed the painstaking task of getting the issues into shape for publication. It has been a complete joy to work with him; I feel fortunate to have him as a colleague.

Ken Brown has been elected as the new editor-in-chief. I am delighted that he has agreed to assume this position and am certain he will do an outstanding job. Contact information for Dr. Brown appears below. We are working to make the transition as smooth as possible. I am also very happy that Cynthia Trowbridge has agreed to assume the responsibility of managing editor. I wish them both the very best!

Janice Voltzow
Editor-in-chief

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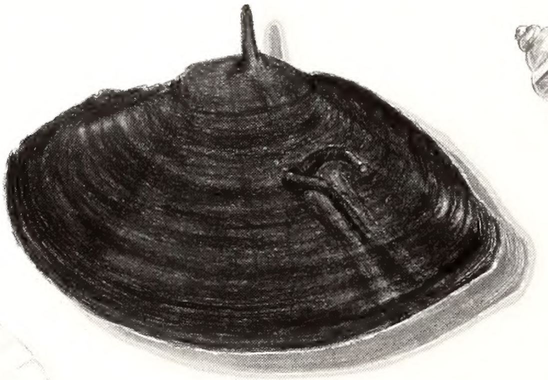
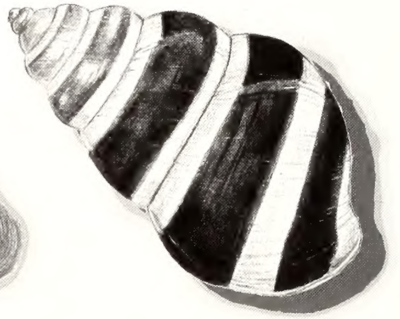
THE MOLLUSKS:
A GUIDE TO THEIR STUDY, COLLECTION, AND PRESERVATION





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C. F. STURM, T. A. PEARCE, and A. VALDÉS

PUBLICATION OF THE AMERICAN MALACOLOGICAL SOCIETY

The Mollusks: A Guide to Their Study, Collection, and Preservation

C. Sturm, T. A. Pearce, and A. Valdés, editors

A new publication from the American Malacological Society

Have you ever wondered about collecting snails with a leaf blower? How about the ins and outs of preserving a giant squid? Do you know what a bail, grab, or box corer are? Maybe you have pondered what types of plastics are safe to use for storing specimens or how to use an optical scanner to image shells. If questions like these arise from time to time, you want a copy of the American Malacological Society's latest publication, *The Mollusks: A Guide to Their Study, Collection, and Preservation.*

The American Malacological Society, founded in 1931 as the American Malacological Union, is an organization that brings together folks interested in mollusks. In 1942, papers presented at the annual meeting in Maine dealt with studying and collecting shells. These papers were published in the Annual Report of 1942 and were reprinted in 1955, 1966, and 1974. With each reprinting, a few more papers from other publications were added. The 1974 booklet, entitled *How to Study and Collect Shells,* was 107 pages in length and had two illustrations. Now, *The Mollusks: A Guide to Their Study, Collection, and Preservations* is the first update of the 1974 booklet in 32 years. If you are looking for a book full of glossy photos, this book is not for you. If you want a book giving the latest information on all modern classes of mollusks and the best methods to study, collect, and preserve them, look no further.

The Mollusks, 445 pages long, with 31 chapters, 101 figures, and 28 tables, is a completely new book. The book was edited by Charlie Sturm, Tim Pearce, and Ángel Valdés. An international team of 29 individuals contributed to these chapters. *The Mollusks* differs in several significant ways from its predecessors.

While the former books were compendia of articles, *The Mollusks* consists of chapters, each covering a specific topic. Some chapters deal with collecting and preserving mollusks, both the shells and soft parts, remote bottom collecting, and SCUBA diving. Other chapters cover archival practices, writing taxonomic papers, the International Code of Zoological Nomenclature, constructing databases, digital imaging, and film photography. Chapter 9 lists over 750 books, monographs, and papers on mollusks indexed by biogeographic region and taxonomic group. If you collected land snails in southern Africa, go to the "Ethiopian (Afrotropic)-terrestrial" listing and you will find a list of 20 books to help you with your material.

All modern classes of mollusks are treated in *The Mollusks.* The Aplacophora, Monoplacophora, Polyplacophora, Scaphopoda, and Cephalopoda have their own chapters. The Bivalvia are covered in three chapters while the Gastropoda are covered in four chapters. There is even a chapter on fossil mollusks. These chapters cover the biology and ecology of these groups, where to find these organisms, and how to collect them. Each chapter has a list of cited references for further information.

The last four chapters of the book cover a variety of topics. Two chapters deal with conservation, one with freshwater mollusks, and the other with marine mollusks. One chapter discusses maintaining a marine aquarium. The fourth chapter is on non-molluscan marine organisms that have calcareous structures and might be mistaken for mollusks.

The Mollusks is a soft covered book retailing for $35.95. For more information and where to order it go to ⟨http://www.malacological.org/publications/molluskguide.html⟩. At this site you will find a link to the publisher's website, here you can read the first chapter of *The Mollusks.* This chapter is a detailed introduction to the rest of the book. Questions about the book can be sent to the editors at doc.fossil@gmail.com.

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Reproductive performance of *Helix pomatia* (Gastropoda: Pulmonata: Helicidae) and survival of its hatchlings under farm conditions

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Abstract: The reproductive ability of 1254 breeding individuals of *Helix pomatia* originating from a local wild population were studied. Reproduction was carried out in a greenhouse at a stocking density of 51.2 breeding snails per m^2. The reproductive season was 83 days long. From 30 May to 21 August 2003 almost all the snails laid eggs at least one time, but 25.1% of the snails laid eggs twice, and 5.2% laid eggs three times. The mean number of eggs per clutch for all the breeding snails was 41.7. Because of the multiple laying of eggs, the number of eggs laid in the 2003 season averaged 61.5 per breeding snail, and the eggs' total biomass constituted 38.5% of the biomass of all breeding individuals. A significant ($P < 0.05$) increase in egg laying was found from 30 May to 21 July. This period was followed by a rapid decline in reproductive intensity, until egg laying ceased on 21 August. Breeding snails laid 77100 eggs, out of which 40000 eggs hatched. From the hatched eggs 27000 two-to-three-week-old hatchlings were obtained. Of the obtained hatchlings 15000 were released into a greenhouse; 32.0% of these individuals survived winter hibernation in a pen. In May of the next year, the 4800 hatchlings were released into a field pen, at a density of 260 specimens per m^2. They reached a mean body mass of 19.1 g and mean shell diameter of 30.1 mm in July. The rapid rate of growth observed under farm conditions allows us to propose a two-year farming cycle for this species, from hatching to the stage of sexual maturity.

Key words: snail breeding, snail growing, snail protection, snail farming

In Poland there are still abundant live natural populations of the Roman snail (*Helix pomatia* Linneus 1758) (Stępczak 1976, Dyduch-Falniowska *et al.* 2001a, 2001b). As it has already happened with *Helix aspersa aspersa* (Müller 1774) and *Helix aspersa maxima* (Taylor 1883), it is likely that specimen numbers in these populations will be in danger of being reduced because of increasing exploitation by exporters for snail meat to other European markets (Łysak 1999). However, over the last 20 years, development of intensive farm-rearing of *Helix aspersa* has been developed, made possible by the snail's high fertility and the recognition of physiological factors and farming technology (Lucarz 1984, Daguzan 1989, Gomot and Gomot 1989, Gomot *et al.* 1989, Gomot and Deray 1990, Lazaridou-Dimitriadou and Bailey 1991). Due to its slower rate of growth, lower fertility, and difficulty with early spring hatching, *Helix pomatia* is regarded as a difficult species to breed compared to *Helix aspersa*. The development of technology for farm-rearing of this species has therefore become not only an economical concern but also an essential matter for environmental protection. Studies on the physiology of the reproductive biology of this species (Jeppensen 1976, Łysak *et al.* 2002) provide the basic background for its intensive cultivation. The aim of the present study was to develop the technology to farm the Roman snail, based on its life cycle and to enhance its rate of reproduction.

MATERIAL AND METHODS

On 25 April 2003, a group of 1254 adult Roman snails, *Helix pomatia*, were harvested from a natural population in a park surrounding the Radziwiłł family residence in Balice, now belonging to the National Research Institute of Animal Production in Kraków (Poland). Snails were placed in a pen in an unheated greenhouse planted with white clover and grass. A hardened and turned-out aperture lip was used as a sign of sexual maturity. The mean body mass of full-grown snails was 21.9 g (SD 3.79, range from 13.88 g to 34.09 g) and the shell diameter was of 34.07 mm (SD 1.77, range from 29.1 mm to 39.2 mm).

Stocking density was 51.2 snails per m^2. Inside the pen, vegetation-free strips of land were left to facilitate the observation of snails laying eggs. In the pen, feed was placed on wooden pallets. A sprinkling system spread water each morning and afternoon. Snails were given extruded vegetable-mineral feed designed for breeding individuals of *Helix aspersa* and produced by the Farming Cooperative in Łubnica (Wielkopolska Province, Poland). The feed was 16.0% soya-bean protein and 12.4% calcium (Ca) in the form of chalk. A detailed composition of the feed was reserved by the manufacturer. Egg laying was monitored every morning. Observations were made on breeding snails that worked their way into the soil to lay eggs. First clutches were laid on 30 May, that is, 35 days after the snails were placed into the greenhouse pen. The last clutches were laid on 21 August. To prevent their escape, laying snails were covered with upturned flower pots. The next day, after egg laying was completed, egg clutches were collected from their hole in the soil. Egg clutches were incubated in soil in plastic trays. Approximately 15000 two-week-old hatchlings were released into a greenhouse pen with a density of 600 specimens per m^2 and fed until late autumn. During the winter, hatchlings hibernated in an unheated greenhouse pen covered with Styrofoam and a gardening fabric used to protect crops from ground frost. In mid-March of the following year, the hatchlings became active and were given snail feed. In mid-April, the protective fabrics were removed to insert wooden feeders. Then, when the spring frosts passed in mid-May, the 4,800 young snails were transferred from the greenhouse to a field pen with a density of 260 specimens per m^2.

Breeding snails that laid eggs were weighed, their shell diameters were measured, and numbers were painted on their shells. Snails were marked to permit further observations of additional egg-laying by marked specimens in the same season. Egg clutches from the marked breeding snails were weighed and egg numbers were counted. From the mass of the clutch and the number of eggs in the clutch, the mean mass of an egg was calculated. These data were used to determine the values of specific reproductive parameters. The increase of body mass and shell diameter of growing snails was meassured in September 2003, and May and July 2004. Each time, random samples of 150 specimens were collected for measurements. Temperature and relative humidity of the air in the greenhouse were measured 20 cm above the surface of the pen. Measurements were taken on workdays at 7:00 and 14:00 hours. The results of reproduction were analyzed using analysis of variance and one-way regression using Statgraphics software.

RESULTS

Microclimatic conditions in the greenhouse pen

Mean air temperature at 7:00 hours decreased from 20.1°C in June to 18.4°C in August, and the temperature at 14 hours ranged from 26.6°C in July to 30.0°C in August. On some days, the afternoon temperature reached 34.3°C in June and 35.9°C in August. There were no significant differences between all mean morning, afternoon, and mean of day monthly temperatures, respectively. Mean humidity of the air in the morning ranged from 77.9% in June to 86.3% in July. In the afternoon, the mean humidity of the air was 65.7% in July, but was only 54.9% and 47.2% in June and August, respectively. There were significant differences ($P < 0.05$) between each mean morning monthly humidity, and highly significant differences ($P < 0.01$) between all mean afternoon and mean daily humidity, respectively. Snails in the greenhouse were active at least until midday, copulating and laying eggs.

Snails were raised under conditions of the natural photoperiod. The natural daylight in June lasted for 16.5-17.0 hours, during July it decreased from 16.5 hours to 15.5, and in August it decreased from 15.5 to 14.0 hours. On 21 August, when the last egg clutches of the season were found, the day length was 14 hours.

Reproductive parameters in the reproductive season

Significantly more snails laid eggs in the period of June-July than in August ($P < 0.01$), when reproductive intensity dropped by 65.7%. (Table 1). An increase in egg laying was found from the start of the reproductive season (30 May) to 21 July. This period was followed by a rapid decline in reproductive intensity, until egg laying ceased on 21 August. In June, the mean number of clutches and eggs laid during 24 hours per m^2 was almost the same as July, while in August this parameter dropped significantly ($P < 0.05$) by 65.5% and 76.2%, respectively. Between June and August, the number of eggs per body mass of parent decreased very significantly ($P < 0.01$) by 38.4%. In successive months, the mean number of eggs per clutch decreased rapidly, and in August the mean number of eggs per clutch was 41.6% significantly lower ($P < 0.01$) than in June. Mean mass per one egg decreased significantly ($P < 0.01$) between June and the period of July-August by 5.0%. The mean mass of clutches declined very significantly ($P < 0.01$) between June, July, and August, by 44.7% during the whole period. The relative mass of a clutch, expressed as a percentage of parental mass, also decreased significantly ($P < 0.01$) by 40.5%.

Significant ($P < 0.05$) and highly significant ($P < 0.01$) negative correlation coefficients were found for the relationship between the egg-laying intensity per 1 day per 1 m^2, and the average body mass and shell diameter of Roman snails laying eggs on a particular day (Table 2). Positive, highly significant correlations were found for the relationship between the individual body mass of a snail and the mean egg mass in the clutch. The same correlation was found for the diameter of the shell in relation to the average mass of a single egg and the mass of a clutch.

Multiple egg laying by the snails during the same reproductive season

Some snails began laying a second clutch of eggs by the middle of June and some began to lay eggs for the third time in late June and in July. In August, only eggs laid by snails laying for the third time in that season were found. During the three months of observation, 25.1% snails laid eggs twice and 5.2% laid three times. The mean interval between the first and the second clutches was 21.7 days; the mean interval

Table 1. Reproduction of *Helix pomatia* housed in a greenhouse pen.

Parameter	Month	Mean	SE	SD	Range
Mean percent of individuals laying eggs per 24 h	June	1.99^{B}	8.61	1.74	0.16-6.06
	July	2.52^{B}	7.85	1.19	0.64-4.78
	August	0.79^{A}	5.48	0.39	0.24-1.36
Mean number of clutches laid per 24 h per m^2 of pen surface area; stocking density was 51.2 snails per m^2	June	1.02^{b}	0.22	0.89	0.08-3.10
	July	1.29^{b}	0.19	0.61	0.33-2.45
	August	0.40^{a}	0.08	0.20	0.12-0.69
Mean number of eggs laid per 24 h per m^2 of pen surface area; stocking density was 51.2 snails per m^2	June	48.81^{b}	11.62	46.48	3.42-163.61
	July	46.52^{b}	8.49	26.85	9.91-102.90
	August	11.33^{a}	2.29	6.62	3.10-19.64
Mean number of eggs laid per 1 g of body mass	June	2.29^{C}	0.05	0.81	0.56-6.11
	July	1.78^{B}	0.06	0.82	0.61-5.63
	August	1.41^{A}	0.07	0.46	0.26-2.40
Mean number of eggs per clutch	June	48.1^{C}	0.88	14.82	14-89
	July	35.9^{B}	1.05	15.47	11-88
	August	28.9^{A}	1.45	10.46	5-67
Mean mass of one egg in clutch (mg)	June	138.7^{B}	1.33	22.11	84-226
	July	133.1^{A}	1.38	19.39	92-200
	August	130.3^{A}	3.33	22.78	85-179
Mean mass per clutch (g)	June	6.57^{C}	0.12	2.07	2.23-13.60
	July	4.72^{B}	0.13	1.93	1.72-13.02
	August	3.63^{A}	0.18	1.20	0.71-6.20
Mean mass of clutch per mass of parent snail (%)	June	30.37^{C}	0.57	9.60	8.09-60.11
	July	23.26^{B}	0.65	9.11	9.28-52.23
	August	18.05^{A}	0.81	5.50	6.11-28.19

a, b, c = significant differences ($P < 0.05$).
A, B, C = highly significant differences ($P < 0.01$).

between the second and the third clutches was 23.2 days. The mean total number of eggs from the three clutches was 117 (range 84-184). All reproductive parameters were higher for the first clutch than for the second. For the mean mass of clutch, differences from first to second and third clutch were highly significant ($P < 0.01$). The same highly significant differences ($P < 0.01$) were observed for mean percentage mass of clutch per mass of parent, and for the number of eggs per g mass of clutch (Table 3).

Reproduction for the entire period of observation

In the entire reproduction season, the mean number of eggs per clutch was 41.7, but the mean number of eggs laid during the entire reproductive period of 3 months was 61.5 per reproductive snail, because 30.3% of the snails laid eggs two or three times during the season. The mean mass of a clutch was 5.6 g, the mean mass of one egg was 132.1 mg, and the mean number of eggs per 1 g of snail biomass was 2.0. Total egg biomass was 38.5% of the total mass of the reproductive adults. In total, the observed snails laid in total 77100 eggs over 83 days, yielding 3145.5 eggs per m^2 of pen.

Rearing performance

Breeding snails laid 77100 eggs, out of which 40000 eggs were hatched. From the hatched eggs 27000 two-to-three-week-old hatchlings were obtained. Of the obtained hatchlings 15000 were released into the greenhouse, from which 7823 specimens or 52.2% of the initial population survived until 15 September.

A total of 4864 individuals released into the greenhouse, 32.4% of the initial population, survived winter hibernation. In May of the next year, the 4800 hatchlings were released into a field pen with a density of 260 individuals per m^2. By September, the mean diameter of the shells of these snails had reached 14.2 mm and the body mass reached 2.5 g. After the winter hibernation, by July 2004, the mean diameter of the shells had reached the minimum of 30.1 mm required in Poland for commercial snails to be collected from natural

Table 2. Results of one-way regression analysis for egg-laying traits of *Helix pomatia,* 1 June to 21 July 2003.

Parameter I	Parameter II	Correlation coefficient (r)	Significance
Number of clutches per m^2 of pen area per day, from 30 May to 21 August	Mean mass of egg-laying snails	−0.68	$P < 0.05$
	Mean diameter of parent shell	−0.71	$P < 0.01$
	Mean mass of egg	−0.71	$P < 0.01$
Number of eggs per m^2 of pen area per day, from 30 May to 21 August	Mean mass of egg-laying snails	−0.67	$P < 0.05$
	Mean diameter of parent shell	−0.67	$P < 0.05$
	Mean mass of one egg	−0.73	$P < 0.05$
Mass of clutch, from 30 May to 21 August	Number of eggs per clutch	0.87	$P < 0.01$
Mass of egg-laying snails	Mass of one egg	0.44	$P < 0.01$
	Mass of clutch	—	not significant
	Number of eggs per clutch	—	not significant
Diameter of parent shell	Mass of one egg	0.48	$P < 0.01$
	Mass of clutch	0.39	$P < 0.01$
	Number of eggs per clutch	—	not significant

Table 3. Reproductive performance of *Helix pomatia* snails which laid eggs 3 times per season.

Clutch number	Mean number of egg per clutch	Mean mass of clutch (g)	Mean mass of clutch per mass of the parent snail (%)	Mean mass of one egg in clutch (mg)	Number of eggs laid per 1 g of body mass
I	49.6	6.8^{A}	32.5^{A}	138.6	2.4^{A}
II	35.2	4.5^{B}	22.2^{B}	131.0	1.7^{B}
III	32.1	4.0^{B}	19.2^{B}	125.0	1.6^{B}

A, B = highly significant differences ($P < 0.01$).

populations. Also at that date, the mean body mass increased to 19.1 g (Figure 1). In April 2004, the coefficients of variation for the body mass and shell diameter were high (80.0% and 26.4%, respectively), due to the two-month differences in age of the hatchlings, which hatched from June to August of the previous year. In July, the coefficients of variation decreased to 33.3% and 11.8%, respectively, because the snails grew.

DISCUSSION

Microclimatic conditions

Gomot (1990) found that under laboratory conditions, Roman snails have the highest reproductive activity when photoperiods last 18 hours. He suggested a the temperature of 20°C partly compensates for the effect of shorter photoperiods on reproduction. A similar effect of higher temperature at shorter photoperiods was found by Jess and Marks (1998) for *Helix aspersa maxima,* and by Gomot *et al.* (1989) for *Helix aspersa.* Similarly, we suspect that greenhouse temperatures in the mornings of June-July 2003, which averaged approximately 20°C compensated for the influence of reduced daylight. In August, however, the natural photoperiod declined below 15 hours, which seemed to cause a rapid decrease in reproductive intensity and termination of egg-laying by snails, despite of the still-high air temperature. Another potential cause of sustained high reproductive intensity in July was the statistically significant higher relative humidity in June than in August. Relative humidity in June was close to the optimal humidity of 75-85% recommended for breading in *Helix aspersa.*

Reproductive parameters in the reproductive season

Roman snails maintained in pens in the field in Poland during June-August 2004 peaked in their reproductive output in June (Chmielewski 2005). The greenhouse pen used in the current study probably provided better microclimatic and feeding conditions for reproduction than was possible in the field pen, and permitted the reproductive intensity in July to remain at the same high level as in June. The reproductive output of the snails in the current greenhouse study

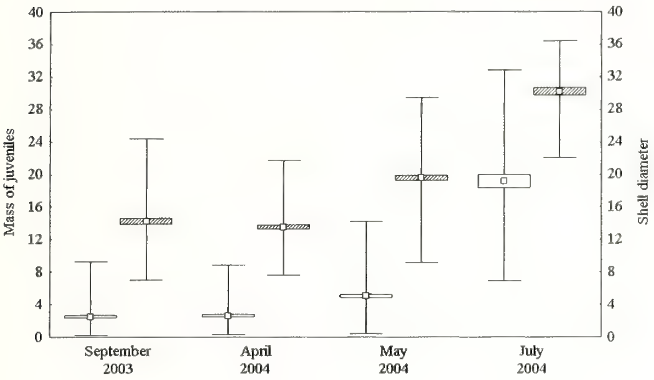

Figure 1. Mean masses (open boxes, in g) and shell diameters (hatched boxes, in mm) of juveniles of *Helix pomatia* hatching from eggs laid in the greenhouse pen in 2003. Box represents ± standard error around mean; whiskers indicate maximum and minimum values.

is similar to that for the month of June of snails maintained under natural conditions (Łysak *et al.* 2001).

Multiple egg laying by the snails during the same reproductive season

In the current study, some individuals laid second and third clutches of eggs in July and in August. Gomot (1990) found that under experimental conditions the frequency of egg-laying by the same snails was higher during a consistent 18-hour photoperiod than during a shorter 8-hour one. Therefore, the repetitive laying of eggs may be a function of both the photoperiod as well as the length of the reproductive season. The first clutches of eggs laid by Roman snails in the season were significantly heavier ($P < 0.01$) and proportionally greater in relation to parental body mass. Clutches of other *Helix* species living in natural conditions and laid at the beginning of the reproductive season also contain more eggs than those laid later in the season (Lazaridou-Dimitriadou and Bailey 1991). However, the clutches of eggs laid later in the season may have been the second and third clutches of the same snails, which may explain why they contained fewer eggs.

Reproduction for the entire period of observation and rearing performance

Our results from rearing older hatchlings, before and after hibernation in the winter of 2003/2004 in a greenhouse pen, and later moving them to a field pen, provides a basis for developing a technology for farming Roman snails over a two-year cycle. Over half of the specimens survived until the time of winter hibernation from the group of two-to-three-week old Roman snails raised in the greenhouse pen 2003, which correspondes to the survival rate required by the technologies for the raising of *Helix aspersa* in its first year of life. We obtained a satisfactory survival rate of 32.0% for the Roman snail hatchlings, calculated from the moment they were placed in the greenhouse pen in the summer of 2003 to the moment they were moved to the field pen in May 2004. The survival rate through July 2004 was lower than the 50% specified by breeding techniques for *Helix aspersa,* but the breeding cycle of the Roman snail is one season longer than that of *Helix aspersa* and it is separated by a period of winter torpor that is physiologically difficult for juvenile snails. The rapid rate of growth observed under farm conditions leads us to propose a two-year farming cycle for this species, from hatching to maturity.

ACKNOWLEDGMENTS

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Determinate growth and variable size at maturity in the marine gastropod *Amphissa columbiana*

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Abstract: Individuals of *Amphissa columbiana* from the intertidal zone of San Juan Island, Washington, U.S.A., typically have either shells with very thin, delicate apertural lips, or shells with thick, robust lips. In laboratory observations, thin-lipped snails grew rapidly but were not sexually mature, while thick-lipped snails grew very slowly or not at all and were sexually mature. These observations are consistent with the hypothesis that *A. columbiana* displays determinate growth, as has been inferred for many columbellids on the basis of intraspecific variation in shell form. Sizes of mature snails were very variable, with the largest individuals weighing 4.5 times more than the smallest (wet weight, excluding shell). I tested the hypothesis that maturation and associated shell thickening are phenotypically plastic responses to the presence of predators. Exposure to effluent from the predatory crab *Cancer productus* in the laboratory had no effect on shell form or relative shell weight (an index of shell thickness), suggesting that this is not the case.

Key words: Columbellidae, shell form, growth, maturation, reproduction

Determinate growth, a pattern of ontogeny in which sexual maturation is accompanied by the cessation of growth, is common among many lineages of animals. In shelled gastropods that display determinate growth, maturation may also be accompanied by changes in the form of the shell aperture (*e.g.*, thickening of the outer lip and formation of a callus on the inner lip; Vermeij and Signor 1992). Many members of the gastropod family Columbellidae display such variation in apertural form within populations, which suggests that they display determinate growth (McLean 1978, Jung 1989, Vermeij and Signor 1992). However, in the absence of data on relationships between reproductive maturity, growth rate, and shell form in any columbellid, other interpretations of variable shell form are plausible. For example, shell form might vary in response to environmental cues like wave force, crowding, food availability, or the presence of predators, and so might not be directly related to maturation (*e.g.*, Wellington and Kuris 1983, Kemp and Bertness 1984, Appleton and Palmer 1988, Trussell 1996). Here I provide data on reproduction and growth that are consistent with the hypothesis of determinate growth in an intertidal population of the columbellid *Amphissa columbiana* Dall, 1916. Shell form thus appears to be a reliable indicator of reproductive status in this species.

The sizes of mature *Amphissa columbiana* in this population were very variable, with the largest mature snails having 4.5 times the body wet weight (excluding shell) of the smallest mature snails. Maturation at small size likely imposes a cost in terms of fecundity per reproductive bout in these snails, and thus requires explanation. I present the results of a laboratory experiment aimed at testing the hypothesis that maturation and associated shell thickening is a phenotypically plastic response to the presence of predators. In this case, the potential reduction in fecundity associated with maturation at small size might be balanced by increased resistance to predation. Exposure to effluent from the predatory crab *Cancer productus* had no effect on shell form or relative shell weight (an index of shell thickness) in *A. columbiana*, suggesting that this is not the case. Determining the causes of variable size at maturity in gastropods with determinate growth, like *A. columbiana*, remains an important problem whose solution will be useful in exploring hypotheses on life history evolution, as well as in interpreting ecological and evolutionary patterns in body size in both fossil and recent assemblages (*e.g.*, Budd and Johnson 1991, Roy 2002).

MATERIALS AND METHODS

Shell form

I studied a population of *Amphissa columbiana* from the intertidal zone of Deadman's Bay, on the west side of San Juan Island, Washington, U.S.A. Identifications were verified by comparison with specimens of *Amphissa* spp. in the collections of the Natural History Museum of Los Angeles County in February 2003, with the assistance of J. McLean.

Shell height (from the apex to the tip of the siphonal canal) was measured with calipers to 0.1 mm. Shell and body weights were estimated in living snails using the method of Palmer (1982). Living snails were weighed while immersed in seawater, blotted dry, and then weighed in air. Twelve thin-lipped and 12 thick-lipped individuals of a wide range of shell heights were measured and weighed as above, then frozen and dissected to separate shell from body tissues. Shell and body tissues were rinsed in fresh water, dried at 65°C for three days, and weighed. Shell weight was related to submerged weight using the ordinary least squares regression: shell weight (g)=1.494* submerged weight (g) −0.002 (r^2=0.999). This regression was used to predict shell weight throughout this study. Body wet weight was calculated by subtracting estimated shell weight from the weight of a snail in air. For this sample of 24 individuals, body wet weight was well correlated with body dry weight (dry weight [g]=0.19* estimated wet weight [g] + 0.001, r^2=0.945), suggesting that body wet weight calculated in this way is a good estimator of body mass.

Growth of thin-lipped and thick-lipped snails

Growth was examined in two sets of laboratory observations made in the winter (during the reproductive season) and spring (after the reproductive season) of 2003. In the first, started in January 2003, 6 thin-lipped (heights 13.2-16.4 mm) and 10 thick-lipped (14.5-16.6 mm) snails were marked by attaching numbered beetags to their shells with cyanoacrylate glue. The snails were measured and weighed as described above, then placed in a plastic container (15 × 15 × 4 cm) with mesh sides submerged in flowing seawater (8-10°C) in a laboratory seatable. The snails were fed muscle tissue from scallops (*Chlamys* spp.) weekly for 10 weeks, after which they were measured and weighed again. The second set of growth observations, started in April 2003, included 11 thin-lipped (heights 12.3-16.4 mm) and 9 thick-lipped (11.1-16.0 mm) snails. After being marked, measured, and weighed, the snails were placed in a mesh-sided container (30 × 18 × 10 cm) submerged in flowing seawater (10-14°C). Snails were fed muscle from *Chlamys* spp. or *Nuttalia obscurata* (Reeve, 1857) 1-2 times weekly for the next 11 weeks, after which they were measured and weighed again. In both sets of observations, food was always present in excess.

Sexual maturity

Maturity of field-collected snails was assessed in two ways. First, I compared lengths of the penises of thin-lipped and thick-lipped snails in a collection of snails made in December 2002 and January 2003 (during the reproductive season). Snails were relaxed in a mixture of equal volumes of seawater and 7.5% $MgCl_2 \cdot 6H_2O$, then fixed in 10% formalin in seawater. Their shells were later removed. Penises were removed from six thick-lipped males, pinned out straight, and measured to the nearest 0.5 mm with a ruler. Penises of the five thin-lipped snails examined were too small to pin out, and were measured without removing them from adults.

Second, I looked for evidence of deposition of egg capsules by snails maintained in the laboratory during the reproductive season. I collected 17 thin-lipped snails and 26 thick-lipped snails in Dec 2002 and sexed them by holding them off the substratum by their shells with forceps and looking for a penis as they extended their bodies from their shells. Most individuals of both groups lacked penises and were assumed to be females. I divided the thin-lipped snails into two separate mesh-walled containers (making sure to include several males in each container), and did the same for the thick-lipped snails. All four containers were submerged in flowing seawater and the snails were fed scallop muscle weekly until March 2003. Containers were examined for the presence of egg capsules at every feeding.

Causes of variation in size at maturity

In a laboratory experiment, I tested the hypothesis that odor cues associated with the presence of crushing predators induce changes in shell form associated with maturation. Because food level has been linked to changes in shell thickness in several snails (*e.g.*, Kemp and Bertness 1984, Boulding and Hay 1993), I also manipulated this variable. In May 1999, I collected 50 thin-lipped *Amphissa columbiana* (shell height 10.5-18.8 mm) from the intertidal zone about 1 km south of Deadman's Bay. These were marked, measured, and weighed. Groups of four or five snails selected to span the size range of collected snails were placed into each of 12 small, mesh-sided containers. Two of these containers were placed in each of six plastic aquaria (20 × 13 × 13 cm). Each aquarium had a separate source of inflowing seawater. Three of the aquaria, "crab" treatments, contained a single individual of *Cancer productus* Randall, 1839 (59-66 mm carapace width). The crab was restricted to the bottom half of the aquarium (away from the snail containers) with rigid plastic mesh. Thus, in the three "crab" aquaria, snails shared a common pool of water with a potential predator. The remaining three "no crab" aquaria were identical to "crab" aquaria except that no crab was included. In each of the six aquaria, snails in one container received food (1/4 of the adductor muscle from a *Chlamys*) weekly (fed treatment); snails in the other container received no food (starved treatment). Containers were cleaned at each feeding. Each crab was fed a single individual of *Chlamys* spp. weekly. When crabs molted, they were replaced with newly collected crabs 55-66 mm in carapace width. Snails were maintained in this experiment for two months, after which they were measured and weighed. During the experiment 8 snails (of the total of 50) died, all of these in fed treatments; these were excluded from analyses. Because of this mortality, the number of snails in each container varied from 3-5, except for one container in which all the snails died. Effects of predator (crab vs. no crab) and food level (starved vs. fed) on relative shell weight (shell dry weight/total weight of the snail) were assessed in a factorial ANOVA.

RESULTS

Shell form

Most individuals of *Amphissa columbiana* exhibited one of two distinct shell morphologies, with a few individuals displaying intermediate forms. In thin-lipped individuals (Fig. 1A), the outer lip of the aperture was extremely thin (50-70 μm) and very delicate, frequently breaking when snails were handled. The outer lip of the aperture was continuously curved, with no straight portions. No denticles were present on either the columellar or outer lips of the aperture, and there was no callus on the columellar lip of the aperture. The remainder of the shell was usually relatively free of epibionts, and the apical whorls were not eroded. Thin-lipped snails were most common deep in crevices and overhangs, and especially under large cobbles at low tide levels. In these habitats, they often occurred in aggregations of up to 20-30 individuals of a variety of sizes. On occasion they were also found singly on exposed rock surfaces.

In contrast, in thick-lipped individuals (Fig. 1C) the outer lip of the aperture was 750-1000 μm thick and very robust. Further, a segment of the outer lip of the aperture—from about 1/3 of the aperture back from the anterior end to about 1/4 of the aperture forward from the posterior end of the aperture—was usually straight and approximately parallel to the coiling axis of the shell. The outer apertural lip bore 15-20 short denticles on its inner surface and several denticles were usually found on the columellar apertural lip as well. A raised callus was present on the columellar lip of the aperture, although it was frequently obscured by encrusting epibionts. At Deadman's Bay, thick-lipped snails were often found in crevices and overhangs and were also relatively common on exposed rocks at low tide. Thick-lipped snails were usually found singly, not in aggregations.

Snails of intermediate shell form (Fig. 1B) were much less common than either thin-lipped or thick-lipped snails. Intermediates had apertures of intermediate thickness, with or without a straight portion of the outer lip of the aperture.

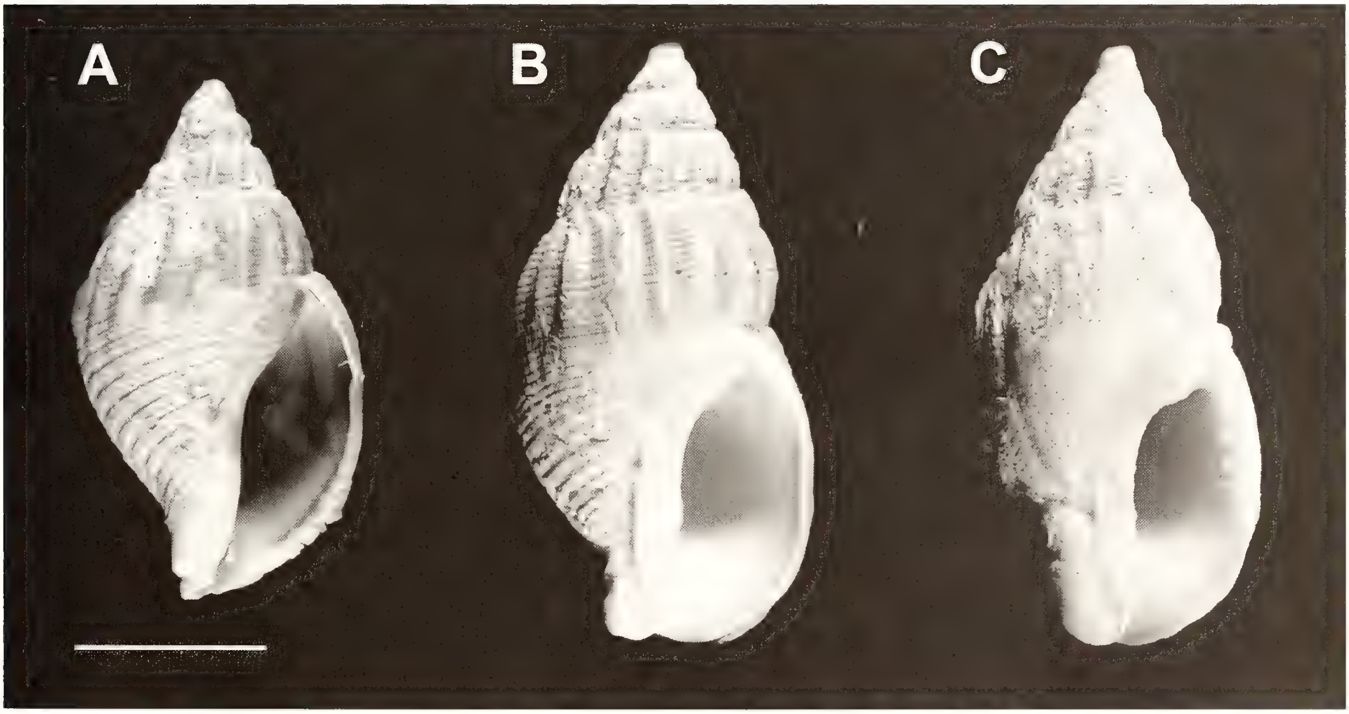

Figure 1. Shells of *Amphissa columbiana* from the intertidal zone of Deadman's Bay, San Juan Island, Washington, U.S.A. A, Thin-lipped individual. Note the continuously curved outer lip of the aperture and the lack of apertural teeth. B, Individual with intermediate shell form. Note the presence of a callus on the columellar lip of the aperture. C, Thick-lipped individual. Note the well-developed teeth, especially on the outer lip of the aperture, the callus on the columellar lip of the aperture, and the greatly thickened outer apertural lip (compare to A). Scale bar=5 mm.

A raised callus was present on the columellar lip of the aperture and apertural denticles were sometimes present (but weakly developed). The shell was usually neither very eroded nor covered with epibionts.

Snails classified according to these criteria also differed quantitatively in allocation to shell and body weight. This is illustrated by data on 74 snails collected in January 2003 (snails collected in 1999 and 2002 showed very similar patterns). Thin-lipped and thick-lipped snails overlapped broadly in shell height (thin 8-18 mm, thick 12-20 mm). ANCOVA of log-transformed data showed that thick-lipped snails had significantly higher shell weight than did thin-lipped snails when shell height was considered as a covariate (Fig 2A; see figure legend for regression parameters). Snails of intermediate shell form fell between thin-lipped and thick-lipped snails. Relative shell weight (shell dry weight/ total weight of the snail) was much higher in thick-lipped snails (67%±2.6% standard deviation) than in thin-lipped snails (52%±4.5%), with snails of intermediate shell form falling in between (62%±6.4%; differences among all three classes of snails significant by ANOVA followed by Fisher's PLSD post-hoc tests, p<0.001). Relative shell weight was unrelated to shell height in intermediate and thick-lipped snails, but negatively correlated with shell height in thin-lipped snails (Fig. 2B). Thus, in addition to qualitative characters, a quantitative index (relative shell weight) could be used to distinguish thin-lipped and thick-lipped snails.

Thin-lipped and thick-lipped snails also differed in relationships between body weight and shell height. ANCOVA of log-transformed data showed that thin-lipped snails had very slightly (but significantly) higher body wet weight than did thick-lipped forms (Fig. 2C). Body weight of the largest thick-lipped snails (0.41 g) was about 4.5 times that of the smallest thick-lipped snails (0.09 g).

Growth of thin and thick-lipped snails

Thick-lipped snails added very little shell or tissue on average (Table 1). Because results from the two observation periods were very similar, I pooled data for thick-lipped snails to test for differences from hypothesized means of zero. In thick-lipped snails, the mean growth increment in shell height was not significantly different from zero (t-test,

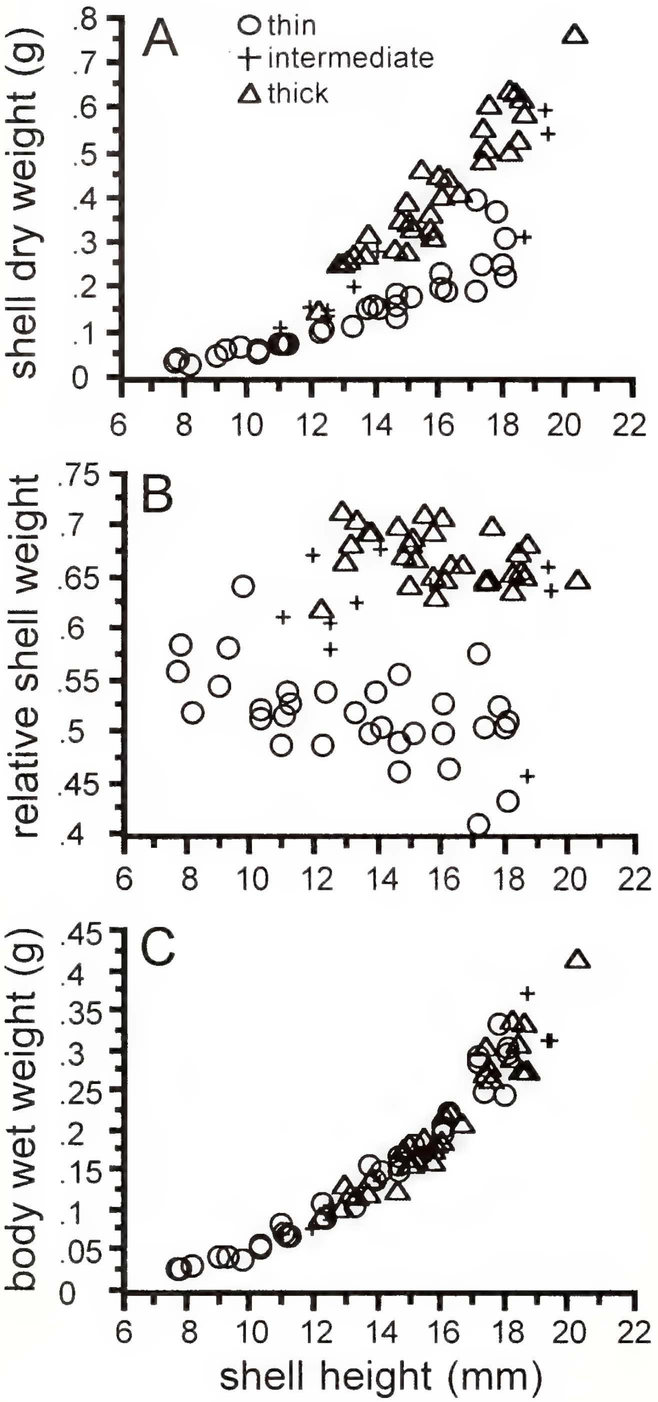

Figure 2. Relationships of shell height with (A) shell dry weight, (B) relative shell weight, and (C) body wet weight for thin-lipped, intermediate, and thick-lipped individuals of *Amphissa columbiana*. Ordinary least squares regressions of log-transformed data showed the following relationships: In (A), for n=32 thin-lipped snails, log (dry shell weight) =2.454 (±0.106) * log (shell height) −3.626 (±0.118), r^2=.947; for n=32 thick-lipped snails, log (dry shell weight) =2.653 (±0.173) * log (shell height) −3.591 (±0.207), r^2=.887 (adjusted means significantly different by ANCOVA, p<0.0001). In (B), for n=32 thin-lipped snails, log (tissue wet weight) =2.818 (±0.069) * log (shell height) −4.064 (±0.077), r^2=.983; for n=32 thick-lipped snails, log (tissue wet weight) =2.945 (±0.134) * log (shell height) −4.247 (±0.161), r^2=.941 (adjusted means significantly different by ANCOVA, p=0.0038). In (C), regression of relative shell weight on shell height is not significant for intermediate and thick-lipped snails (p=0.54 and 0.06, respectively), but it is significant for thin-lipped snails (n=32, relative shell weight =0.614 −0.007 * height, r^2=.266).

Table 1. Initial sizes and changes in size of thin-lipped and thick-lipped individuals of *Amphissa columbiana* held in a common laboratory environment. Two sets of observations of growth increment were made, the first starting in January 2003 (during the reproductive season) and the second in April 2003 (after the reproductive season). Changes in size are reported as means (standard deviation).

January-March observations (10 weeks)					
Shell form	n	Initial height (mm)	Change in height (mm)	Change in shell weight (g)	Change in body weight (g)
Thin-lipped	6	14.48 (1.187)	4.8 (1.58)	0.128 (0.021)	0.225 (0.093)
Thick-lipped	10	15.47 (0.785)	0.06 (0.18)	0.004 (0.004)	0.007 (0.007)
April-July observations (11 weeks)					
Shell form	n	Initial height (mm)	Change in height (mm)	Change in shell weight (g)	Change in body weight (g)
Thin-lipped	11	13.49 (0.686)	5.9 (1.87)	0.197 (0.043)	0.238 (0.105)
Thick-lipped	9	14.32 (1.672)	0.0 (0.15)	0.007 (0.007)	0.009 (0.008)

p=0.16), but mean growth increments for shell mass and body mass growth were very slightly greater than zero (t-tests, p<0.001). Thin-lipped snails grew very rapidly (Table 1), with many individuals adding more than a whorl of new shell during these observations. There were no obvious differences between growth increments of thin-lipped snails measured during the reproductive season versus those measured after the reproductive season. Growth increments for all three parameters were significantly greater in thin-lipped snails than in thick-lipped snails in both sets of observations (t-tests, p<0.005).

Sexual maturity

Penises of six thick-lipped snails (shell heights 19.0-22.1 mm) ranged from 10-12 mm in length (mean 11.2 mm), while penises of five thin-lipped snails (shell heights 14.1-20.3 mm) ranged from 1-3 mm in length (mean 1.7 mm). Thus, penises of thick-lipped snails were on average about seven fold longer than those of thin-lipped snails (difference significant by t-test, p<0.001).

None of the 17 thin-lipped snails observed in the laboratory during the reproductive season of 2002-2003 deposited egg capsules. In contrast, many egg capsules (indicating deposition by multiple females) were observed in both of the chambers containing thick-lipped snails.

Causes of variation in size at maturity

Food availability had clear effects on growth (expressed as percent change) in shell height, shell weight, and body weight (Fig. 3A). These effects were in the expected direction—fed snails grew much more than did starved snails. In contrast, presence or absence of crabs had no obvious effects on snail growth.

By the qualitative criteria described above, shell form in experimental snails did not change during the experiment—no snails obviously switched from the thin-lipped to the thick-lipped morph. Predator treatment had a nearly significant effect on an index of shell thickness, relative shell weight, when raw data were used in the analysis (F=3.84, degrees of freedom 1, 38; p=0.057; Fig. 3B). When container means were used in place of raw data (a modification of the analysis that reduces its power, but also reduces the chances of Type I error), predator treatment had no significant effect on relative shell weight (F=1.46, d.f. 1, 7; p=0.267).

Food availability had a significant effect on relative shell weight regardless of whether raw data or container means were used in the analysis (raw data F=27.06, d.f. 1, 38; p<0.0001; container means F=14.08, d.f. 1, 7; p=0.007). At the beginning of the experiment, for all snails, shell comprised a mean of 50.3±5.0% of total snail weight. At the end of the experiment, starved snails had a higher mean relative shell weight (54.2±4.5%) than fed snails (47.4±4.5%; Fisher's PLSD post-hoc test for container mean data, p=0.008; Fig. 3B).

DISCUSSION

Determinate growth explains striking variation in shell form in the intertidal gastropod *Amphissa columbiana* (Fig. 1). Young snails build thin-lipped shells and grow rapidly, but eventually they alter the shape and thicken the apertures of their shells and grow only very slowly, if at all (Table 1). These differences in shell form and growth rate are correlated with differences in sexual maturity. Male thick-lipped snails have large penises, while the penises of thin-lipped snails are so minute that they are likely not functional in copulation. Thin-lipped snails maintained in the laboratory did not deposit egg capsules, while thick-lipped snails deposited many egg capsules, suggesting that female thin-lipped snails are not sexually mature. However, in these experiments, female thin-lipped snails were only offered thin-lipped males (which have tiny, probably nonfunctional penises) to mate with, so an alternative hypothesis is that female thin-lipped snails were sperm-limited. Although I studied patterns of shell form, growth rate, and maturity in

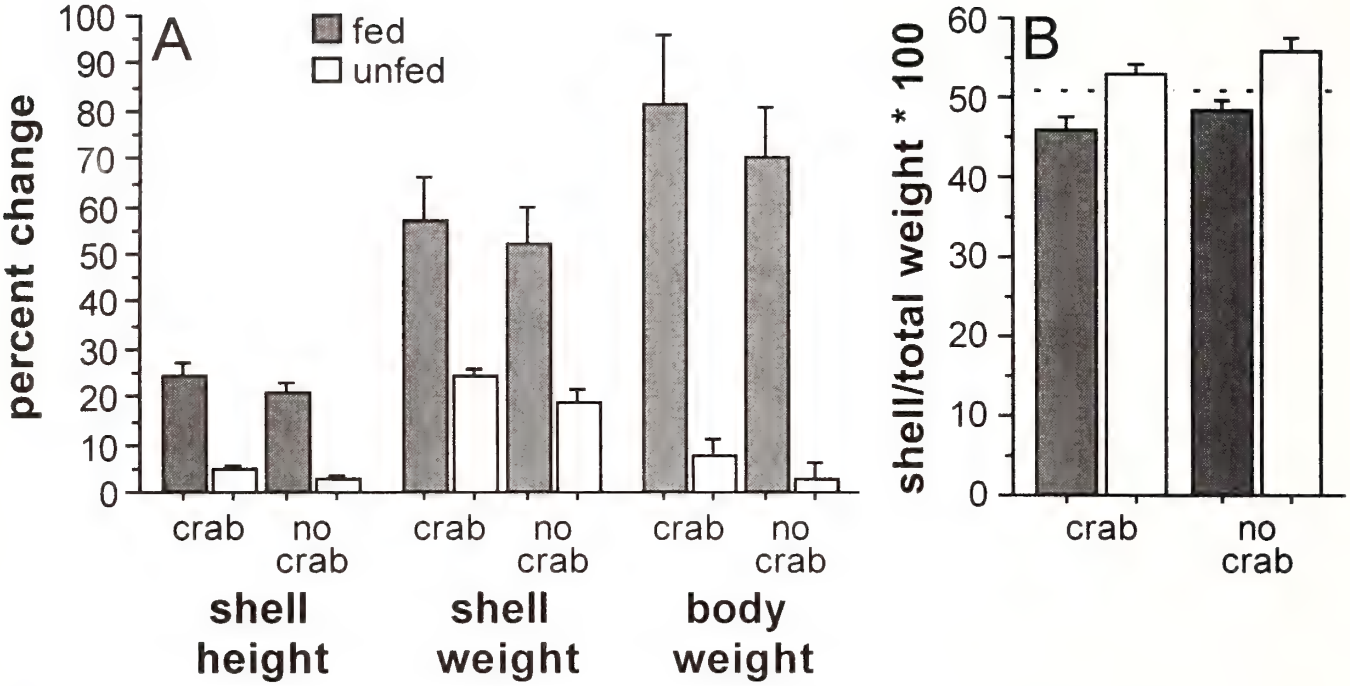

Figure 3. Percent change in (A) shell height, shell weight, and body weight and (B) relative shell weight (shell weight/total weight) in individuals of *Amphissa columbiana* after two months of rearing under different conditions in the laboratory. Means (± standard error) are shown, with n=8-14 replicate snails for each bar. The dashed line in (B) represents the mean relative shell weight of all snails at the beginning of the experiment.

only one intertidal population, both thin-lipped and thick-lipped snails are also present in intertidal populations elsewhere in Washington State and in subtidal populations in the San Juan Islands (personal observation). In these populations as well, similar differences in shell form are likely attributable primarily to determinate growth. To my knowledge, these are the first data on growth and reproduction applied to testing the hypothesis of determinate growth in columbellids. Determinate growth in the family has previously been inferred solely from variation in shell form (McLean 1978, Vermeij and Signor 1992).

In a popular guide to shells, White (1976) mentioned variation in shell thickness in intertidal populations of *Amphissa columbiana*, but interpreted it with the hypothesis that *A. columbiana* "develops thicker shells where exposed to wave action." The variability he mentioned (but did not describe further) may simply have been normal ontogenetic variation in shell form and thickness like that described here. It is possible that shell form in *A. columbiana* varies both ontogenetically and with environmental conditions like wave action, but further studies comparing shell form among populations exposed to different environmental conditions are needed to clarify this issue. Tupen (1999) described substantial site-associated quantitative variation in adult shells of another columbellid, *Alia carinata*. A plausible explanation for such variation is phenotypic plasticity, similar to that suggested by White (1976).

It is interesting to note that collections of post-mortem shells of *Amphissa columbiana* may, depending on their provenance, represent strongly biased samples of life history stages and shell sizes. For example, assemblages of post-mortem shells of *A. columbiana* present on the shore at Deadman's Bay (almost all occupied by hermit crabs) are mostly those of thick-lipped snails greater than 13 mm in height (personal observation). The rarity of thin-lipped shells of juvenile snails in these assemblages may be a result of low mortality among juvenile snails (*e.g.*, because they tend to inhabit protected microhabitats), greater vulnerability of juvenile shells to shell-destroying predators, or rapid post-mortem degradation of thin-lipped shells. Collections made from natural assemblages of dead shells are very likely to reflect a bias towards the shells of larger, mature snails. For similar reasons, the delicate juvenile shells of *A. columbiana* (and perhaps other determinately-growing columbellids) may also be less likely to be preserved as fossils than are robust adult shells. Such potential sampling and taphonomic biases should be taken into consideration when making inferences from shell form in determinately-growing snails.

If, as argued above, thickening of the shell aperture and cessation of growth is correlated with maturation in *Amphissa columbiana*, then size at maturity varied over a range of about 1.7-fold as shell height and 4.5-fold as wet body weight in the Deadman's Bay population. This wide range in size within a single population of a single species represents about 22% of the total range of adult sizes of 144 species of columbellids studied by Roy (2002). (Roy used the geometric mean of shell height and width as an index of size, and I estimated this index for small and large adult individuals of *A. columbiana* for comparison with his data.) Such great variability in adult size appears to be fairly common among determinately-growing gastropods (Vermeij 1980). Although no data are available on the relationship between body size and fecundity in *A. columbiana*, by analogy with other gastropods (*e.g.*, Iyengar 2002, Angeloni 2003) the two are very likely correlated. The fecundity of small *A. columbiana* is thus probably limited relative to that of large individuals. What causes many snails in this population to mature and stop growing at small sizes?

Some component of the observed variation in size at maturity is likely to be genetic (*e.g.*, Richards and Merrit 1975, Brown *et al.* 1985) and might be identified in breeding studies. Size at maturity might also vary as a plastic response to several environmental variables, such as food quantity or quality, or risk of predation or parasitism (*e.g.*, Brown 1985, Brown *et al.* 1985, Lafferty 1993). I examined whether one of these environmental factors, the presence of odor cues associated with a crushing predator, affects the timing of maturation and shell thickening in *Amphissa columbiana*. High risk of predation might induce early maturation in *Amphissa columbiana* because this would improve the chances of reproduction before death, but also because shell thickening, which is associated with maturation, is expected to render shells more resistant to attack by shell-crushing predators (*e.g.*, Palmer 1985, Vermeij and Signor 1992, Trussell 2000). My results suggest that odor cues associated with a potential crushing predator (the crab *Cancer productus*) do not induce maturation and shell thickening in *Amphissa columbiana* (Fig. 3). There were no qualitative changes in the form of thin-lipped snails raised in the presence of crabs. Whether or not *C. productus* was present, thin-lipped fed snails increased in shell weight by a mean of about 55% of their initial shell weight over 8 weeks (Fig. 3A). Because fed snails added even more body weight over the course of the experiment (roughly 75% of initial body weight, Fig. 3A), relative shell weight, an index of shell thickness, decreased slightly over the course of the experiment (Fig. 3B). This index was expected to increase if snails thickened their shells in response to crab-associated odor cues. Addition of 55% of initial shell weight, if allocated primarily to thickening the shell instead of to continued spiral growth, would be nearly sufficient to fully convert a thin-lipped to a thick-lipped snail (Fig. 2).

This result has many possible interpretations. One is that odor cues associated with predators genuinely do not affect the timing of maturation in *Amphissa columbiana*. Alternatively, predator cues may have been too weak to elicit a response in experimental snails; snails may respond to predators other than small *Cancer productus*; or snails may respond to a correlate of predator presence (*e.g.*, the smell of crushed conspecifics) instead of to predator odor itself. However, *C. productus* is known as an important crushing predator of intertidal snails of a wide range of sizes (*A. columbiana* falls within that size range: Palmer 1985, Boulding *et al.* 1999) in similar habitats in the northeast Pacific. *Nucella lamellosa* (Gmelin, 1791) reared under similar conditions to those described here alter shell form in the presence of odor cues from *C. productus* within 2.5 months (Appleton and Palmer 1988), suggesting that sufficient predator cue and time was allowed in my experiments to elicit a response if it existed. In *N. lamellosa*, the effect of crab odor is enhanced when the *C. productus* are fed conspecific snails, but is detectable no matter what the crabs are fed (Appleton and Palmer 1988). These considerations lead me to favor the first interpretation, that size at maturation in *A. columbiana* is genuinely not affected by the presence of cues associated with predators.

Regardless of the presence or absence of predator odor cues, food level had a small but significant effect on relative shell weight in *Amphissa columbiana*. Both fed and starved snails grew during these experiments, but in fed snails, more of the increase in total weight was allocated to the body tissues than the shell, leading to a decline in relative shell weight. In starved snails (which grew much less than fed snails), more of the increase in total weight was due to increased shell weight, leading to a slight increase in relative shell weight (Fig. 3). It seems likely that this increase in allocation to shell is not associated with maturation, but instead is related to slow growth (*e.g.*, Kemp and Bertness 1984; Boulding and Hay 1993). However, habitat quality (of which food quantity and quality is a major part) has been associated with age and size at maturation in several other gastropods (*e.g.*, Vermeij 1980, Brown 1985, Lafferty 1993) and with other changes in shell form in other species (*e.g.*, Appleton and Palmer 1988).

Another way of identifying environmental cues that might affect size at maturation is to examine variation in adult size among habitats. Tupen (1999), for example, found significant differences in shell dimensions among populations of another columbellid, *Alia carinata* (Hinds, 1844), from several different habitats. He argued that these differences might have resulted from phenotypic plasticity or post-settlement selection on the basis of habitat-specific differences in predation or wave exposure. No comparable studies have been carried out for *Amphissa columbiana*. However, individuals of *A. columbiana* from some subtidal habitats in the San Juan Islands may reach much larger adult sizes than those in the intertidal zone at Deadman's Bay. At the latter site, I have not seen snails larger than 21 mm shell height in five years of observations, but among the 7 subtidally collected specimens in the Friday Harbor Laboratories Synoptic Collections, 4 have shell heights greater than 25 mm, with one snail whose apertural lip is of intermediate thickness measuring 28.7 mm. *A. columbiana* have planktonic, feeding larvae that spend at least two weeks in the plankton (personal observation) so subtidal and intertidal populations are likely well-mixed genetically. These data suggest that environmental differences between intertidal and subtidal habitats affect size at maturation in *A. columbiana*.

Individuals of *Amphissa columbiana* that were kept in the laboratory for two months without food grew substantially, adding on average about 20% to their initial shell weight and about 5% to initial body weight (Fig. 3). It is not clear what fueled the growth of starved snails. Shell growth was not occurring at the expense of body weight, as both increased over the course of the experiment. Similar increases in shell weight in the face of starvation have been recorded previously in *A. columbiana* (and other snails: Palmer 1983), although in that study body weight is not reported. Hatfield (1979) found that another columbellid, *Anachis avara* (Say, 1822), increased in shell height by about 10% over six weeks of starvation, and suggested that particulate or dissolved organic matter present in the seawater fueled this growth. This may be the case for *A. columbiana* as well. My data (Fig. 3) suggest a trend of higher overall growth for snails raised in the presence of crabs versus those raised without crabs. It is possible that some bivalve tissue was torn into small bits by crabs (all of which were fed) and was carried by water into snail containers. However, starved snails reared in the absence of crabs (and in the absence of crab food) also increased in both shell and body weight.

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Land snail diversity in subtropical rainforest mountains (Yungas) of Tucumán, northwestern Argentina

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Abstract: A survey of the micro-land snails in the mountain rainforest or "Yungas" of Tucumán Province, Northwestern Argentina (26°20′-27°30′S) was carried out. A total of 75 samples were processed from 25 stations of 10 × 10 m each. We identified the snails collected to species level and built a species per station data matrix to analyze patterns of diversity. Non-parametric estimators (ICE and Chao2) using EstimateS 5.0.1 were used to estimate the true diversity of the area, the degree of undersampling, and spatial aggregation in the data. Other diversity measurements such as Shannon and Whittaker indices were also calculated. Our study estimated the micro-mollusc species richness of the Yungas of Tucumán to be 21 species distributed among 9 families, with a notably high number of specimens collected (7741). The most speciose family was Charopidae with a total of seven species identified. However, the most abundant families were Diplommatinidae and Systrophiidae. *Adelopoma tucma* and *Wayampia trochilioneides* were the most abundant species, the least frequently found species was *Lilloiconcha tucumana*. The non-parametric estimators showed that our survey was complete and that patchiness did not affect diversity estimations. San Javier and Escaba stations had the highest species richness, the most diverse station was Escaba. Most previous studies in other places in the world show high species richness and low density of specimens. In Tucumán, on the contrary, the absolute abundance of specimens was high with a low species richness.

Key words: Species richness, micro-molluscs, taxonomy, *Adelopoma*, South America

The subtropical mountain rainforest or "Yungas" in northwestern Argentina ranges from 300 to 2000 m above sea level, in areas where it rains more than 1000 mm annually (Brown and Grau 1995). Grassland areas distributed above 1800-2000 m are often included in this ecoregion, although they have a completely different kind of vegetation from that characteristic of the Yungas. The Yungas, together with the rainforest of the Paranaense region (Northeastern Argentina), represents less than 2% of the surface of Argentina but contains more than 50% of the biodiversity present in this country. The Yungas, also known in Argentina as "Tucumano-Boliviano" rainforest, are latitudinally distributed along a narrow area in the northwestern part of the country from the boundary with Bolivia (S 22°) to southern Catamarca province (S 28°). One of the reasons for the comparatively high diversity of flora and fauna reported in the Yungas is the marked altitudinal variation that occurs in this region. The flora comprises three well differentiated altitudinal zones having distinct physiognomies and floras.

Huge areas of the Tucumano-Boliviano rainforest were already degraded or profoundly altered before basic information on biodiversity, including a complete inventory of molluscan species, could be obtained. Detailed data on diversity of undisturbed forest faunas are therefore urgently needed. Our lack of knowledge on biodiversity is particularly apparent concerning invertebrate taxa, especially land molluscs (de Winter and Gittenberger 1998, Myers *et al.* 2000). The micro-snails are poorly studied in most forest regions of South America. This situation is worsened because specimen representation of the local fauna in malacological collections is also inadequate, due to the limited funds available for taxonomic studies (Wheeler 2004). Limited taxonomic and ecological information of most land snail groups distributed in South America make it almost impossible to incorporate this group of invertebrates into plans of conservation (Myers *et al.* 2000, Lydeard *et al.* 2004). One of the present prejudices is the statement that land snails are neither diverse nor abundant in ecosystems like tropical and subtropical rainforests due to their type of soil and weather (Solem 1984). Solem stated that the lack of nutrients and litter and the abundance of predators on the molluscan fauna make the tropical rainforest an unfavorable habitat for snails. On the contrary, other environments with stable temperatures, moderate moisture, and rich soil litter are habitats with the highest diverse land snail faunas. Several studies around the world (in Madagascar [Emberton 1995, Emberton *et al.* 1996, 1999], Mexico [Naranjo and García 1997], French Guyana [Gargominy and Ripken 1998], Cameroon [de Winter and Gittenberger 1998], Kenya [Tattersfield *et al.* 2001], and Venezuela [Martínez 2003]) have tried to test Solem's hypothesis with respect to the environmental conditions. Most of them concluded that in fact tropical rainforests can contain very speciose gastropod faunas. Nevertheless, very little information for comparisons exists with respect to subtropical rainforest areas, where the floral composition, weather conditions, seasonality, and type of soil differs considerably from tropical areas. Moreover, a progressive decline in richness and abundance of characteristic tropical land snail groups inhabiting northern and central South America (*e.g.*, Systrophiidae, Streptaxidae, Neocyclotidae) towards lower latitudes and the eventual replacement of these groups by others inhabiting southern subtropical rainforest habitats is a process not clearly documented nor understood. It is also not clear if the decline of species richness along a latitudinal gradient proposed for vertebrates is also valid for most invertebrates including land molluscs but excluding arthropods (Longino *et al.* 2002). Even if this latitudinal gradient in South America would also be valid for land snails, the causes in the changes of species richness and species turnover have not yet been hypothesized.

This study aimed to: (1) Determine the taxonomic composition of the micro-molluscan fauna from the Yungas in Tucumán, (2) Establish the species richness (gamma diversity) of this ecoregion, which is the result of the alpha (within community) and beta (variation of species composition among communities) diversities, and (3) Compare these results with the species richnesses and abundances reported for other parts of the world, especially the southern hemisphere.

MATERIALS AND METHODS

Study area

Our field research was carried out in the biogeographic region of the Yungas or Tucumano-Boliviano rainforest in Tucumán Province, northwestern Argentina (26°15′-27°40′S). This area corresponds to the southernmost extension of the Andean Neotropical Montane Forest (Cabrera 1971, Cabrera and Willink 1973). Precipitation in the Yungas is characterized by a monsoonal regime with rainfall concentrated in the summer and early autumn months (November-April) (Grau and Veblen 2000). The Yungas ecoregion is usually divided into three altitudinal vegetation zones (Brown and Grau 1995, Valdora and Soria 1999). The Piedmont Forest located from 400 to 700 m above sea level consists of the basal portion of the Yungas, with an annual precipitation of about 600 to 1000 mm. It is also called "Transition rainforest" (Cabrera 1971, Prado 1995). It is mainly characterized by deciduous trees and a low abundance of epiphytic vegetation. Some of the most common trees are *Tipuana tipu* (Benth, 1898) (common name: "tipa"), *Enterolobium contortisiliqum* (Vellozo, 1892) ("pacará"), *Phoebe porphyria* (Grisebach, 1889) ("laurel"). The degradation process (*e.g.,* over explotation, fires, crops) produced great structural transformation of the piedmont rainforest into xerophilic woods (Brown and Grau 1995). This basal zone of the Yungas is the most affected by human activity in Tucumán. The Lower Montane Forest extends from 700 to 1500 m, with an annual precipitation between 1500 and 3000 mm. Some of the most characteristic trees of this altitudinal zone are *Tipuana tipu* (Beth, 1898) ("tipa"), *Jacaranda mimosifolia* Don, 1822 ("tarco"), *Phoebe porphyria* (Grisebach, 1889) ("laurel"), *Myrcianthes uniflora* (Linné, 1773) ("arrayán") and *Blepharocalyx gigantea* Lillo, 1911("horco molle"). Above 1500 m is the Upper Montane Forest, with an annual precipitation between 900 and 1300 mm. This zone is characterized by the presence of *Podocarpus parlatorei* Pilger, 1903 ("pino del cerro"), and *Alnus acuminata* (Kunth, 1904) ("aliso").

Sampling

The material used in the present study consisted of adult terrestrial micro-molluscs from different taxonomic groups. Micro-molluscs or micro-snails are defined as those species that as adult have shells not larger than 5 mm maximum dimensions. Molluscs larger than 5 mm, informally called macro-molluscs, were not considered in the present study because they were too low in abundance and patchily distributed to be adequately sampled by our methods. Thus we excluded *Epiphragmophora* Doering, 1874, *Scutalus* Albers, 1850, *Drymaeus* Albers, 1850, and specimens of Veronicellidae. All of the specimens of micro-snails collected were deposited at the Fundación Miguel Lillo Malacological Collection, Tucumán, Argentina. The methodology used in the present study was adapted from those of Emberton *et al.* (1996) and de Winter and Gittenberger (1998). We sampled 25 stations consisting of a 10 × 10 m patch during the summer season when land snails are more active in Tucumán Province (Fig. 1, Table 1). Within each station we qualitatively searched for micro-snails for half an hour in selected microhabitats that seemed the most favorable for them, such as between exposed roots of trees where dead organic material usually accumulates and under and between dead tree trunks lying on the forest floor. In each station we also took three samples of 50 × 50 cm quadrats of leaf litter plus 2 cm of topsoil from moist, sheltered microhabitats so that a total of 75 samples were processed from the total of 25 stations. Because land snails are generally distributed in patches, it seemed more appropriate to take samples from places most suitable for them. For each station we recorded the altitude (Thommen altimeter), latitude and longitude (Garmin GPS), general topography, and kind of vegetation. Leaf litter plus topsoil samples were placed in plastic bags and kept as cool as possible (10-15°C) in the laboratory no longer than one week until processing. Each bag was opened daily for

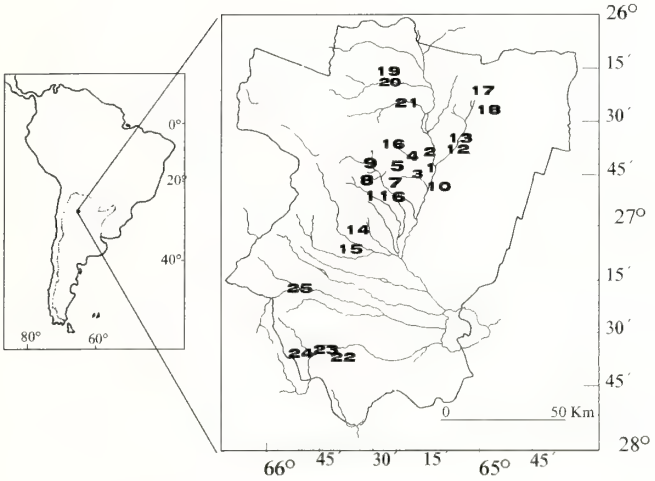

Figure 1. Map of Tucumán province indicating the 25 sample stations located in 15 geographic localities. Station numbers correspond to those listed in Table 1.

aeration. The qualitative search provided more living specimens in most of the stations than did the soil plus leaf litter samples. All snails found alive were relaxed in deoxygenated water for 24 hours and then preserved in 90% ethanol. Soil plus leaf litter samples were dry-sieved through three decreasing mesh widths (3 mm, 1.5 mm, and 0.5 mm) in the laboratory. The three samples from the same station search were treated together for the statistical analysis because there were no differences in the species composition nor in the abundance of specimens among them. After the process of separation of soil and snails, shells were sorted and identified using a Leica MZ6 stereoscopic microscope. An altitudinal transect from 800 to 1460 m was carried out in the Sierra de San Javier locality (Stations 1-5). In this transect the stations (five in total) were sampled every 100 m of elevation to estimate the possible altitudinal variation of the community in the different vegetation zones of Yungas.

Taxonomic identification

Specimens were identified based on shell characters only, except in the case of *Wayampia trochilioneides*

Table 1. Stations (Sn) sampled for micro-molluscs in Tucumán. T_s = total number of species collected per station. T_{ind} = total number of specimens collected per station. PF = Piedmont Forest, LM = Lower Montane Forest, TF = Transition Forest, UM = Upper Montane Forest.

SN #	Name	Elevation (m)	Latitude S	Longitude W	Rainfall (mm/year)	T_s	T_{ind}	Type of vegetation
1	Nina's road, San Javier Mountain	920	26°43′11″	65°17′35″	1505	14	565	PF
2	Nina's road, San Javier Mountain	1020	26°43′07″	65°18′02″	1505	14	289	LM
3	Nina's road, San Javier Mountain	1120	26°43′11″	65°18′17″	1505	14	688	LM
4	Nina's road, San Javier Mountain	1210	26°43′09″	65°18′33″	1505	14	386	LM
5	Nina's road, San Javier Mountain	1460	26°42′54″	65°18′47″	1505	7	15	UM
6	Horco Molle, Yerba Buena Dept.	940	26°51′32″	65°25′32″	1500-2000	11	211	PF
7	Estancia San Javier, Tafi Viejo Dept.	1050	26°46′26″	65°23′24″	1173	12	173	LM
8	Potrero de Las Tablas, Lules Dept.	750	26°46′16″	65°25′34″	1083	11	809	PF
9	Potrero de Las Tablas, Lules Dept.	800	26°46′16″	65°25′34″	1083	9	115	PF
10	San Miguel de Tucumán, Capital	450	26°48′26″	65°14′58″	986	4	82	PF
11	Raco, La Hoyada	880	26°46′16″	65°28′04″	694	11	270	LM
12	El Cadillal, Aguas Chiquitas	515	26°36′48″	65°11′11″	1096	13	352	PF
13	El Cadillal, Aguas Chiquitas	560	26°36′51″	65°11′11″	1096	12	362	PF
14	Tafi del Valle	550	27°05′43″	65°37′10″	900	7	138	PF
15	Tafi del Valle	900	27°03′22″	65°40′20″	800-1000	10	148	LM
16	Villa Nougues	1200	—	—	1173	7	55	LM
17	Medinas Mountain, Buruyacu Dept.	1200	—	—	—	4	141	LM
18	Timbó Viejo, Burruyacu Dept.		26°26′28″	64°59′43″	—	7	245	TF
19	Gonzalo, San Pedro de Colalao	1250	26°18′40″	65°31′45″	600-800	9	445	LM
20	Hualinchay, Trancas Dept.	1360	26°19′35″	65°2′21″	700-900	10	687	LM
21	Rearte, Trancas	1370	26°21′05″	65°32′25″		5	16	TF
22	Escaba abajo, Juan Bautista Alberdi	600	27°38′57″	65°44′46″	1119	10	88	PF
23	Escaba abajo, Juan Bautista Alberdi	650	27°40′02″	65°45′40″	1119	13	681	PF to LM
24	Escaba arriba, Juan Bautista Alberdi	700	27°39′14″	65°46′11″	1119	12	491	PF to LM
25	Cochuna	1235	27°19′41″	65°55′33″	1400-1600	10	253	LM

(d'Orbigny, 1835), for which anatomical dissections were also used. Only specimens with complete shells were considered. Some shells from species difficult to identify were mounted on stubs, sputter coated, and observed with a Jeol 35CF scanning electron microscope. We identified the material collected to species level and built a species per station data matrix to analyze patterns of diversity. For the taxonomic identification we used the available regional identification keys (Fernández and Castellanos 1973) plus the original species descriptions. We followed the general classification for Neotropical micro-molluscs of Muller da Fonseca and Thome (1993) and a general classification of Gastropoda by Wade *et al.* (2001).

Diversity measurements

To estimate the true number of species in the community, we used non-parametric estimators of diversity calculated with EstimateS, version 5.0.1 (Colwell 1997). EstimateS uses the relative abundance of rare species to estimate the number of species not seen. EstimateS was also employed to assess the degree of undersampling and spatial aggregation in the data. This program computes randomized species accumulation curves and reports the means of various statistics based on those curves (Heyer *et al.* 1999). A species-accumulation curve is a plot of the accumulated number of species found with respect to the number of units of effort expended. In the present study, the effort is of a discrete-type (samples). The species-accumulation curve for a highly undersampled fauna will appear nearly linear, with each sample adding many new species to the inventory. On the contrary, the curve for a thoroughly sampled fauna will reach a plateau, with few or no species being added with additional sampling (Longino 2000). We treated the data as presence and absence scores of species by samples. The estimator chosen in the present study for non-parametric richness estimation were the Incidence-based Coverage Estimator (ICE) (Lee and Chao 1994) and the Chao2 estimator (Chao 1987). Relying on the concept that rare species carry the most information about the number of missing ones, Chao uses only singletons and doubletons to estimate the number of missing species. When the abundance-based coverage estimators (ACE) were used, transforming the former matrix by adding the abundance of each taxon per sample, similar curves were obtained. We used the default values for number of randomizations (50) and cutoff values for coverage-based estimators (10). Both estimators, ICE and Chao2, augment the negatively biased observed richness by a factor that depends on the presence of and distribution within samples of "rare" taxa. For the estimator used, the "rare" species are those observed in only one or two samples (ICE is more complex but the logic is the same). When all species in the data matrix had been observed multiple times, the inventory is complete but when inventories are replete with "rare" species, true richness is underestimated. EstimateS 5.0.1 include techniques to assess graphically the degree of spatial aggregation in the data. For this purpose a Coleman curve (rarefaction curve) was also calculated (Fig. 2). Coleman curves are not estimators of species richness in the same sense as the other estimators. While Chao2 and ICE estimate total species richness, rarefaction curves estimate sample species richness from the pooled total species richness (Colwell 1997). Rarefaction curves represent the means of repeated re-sampling of all pooled samples.

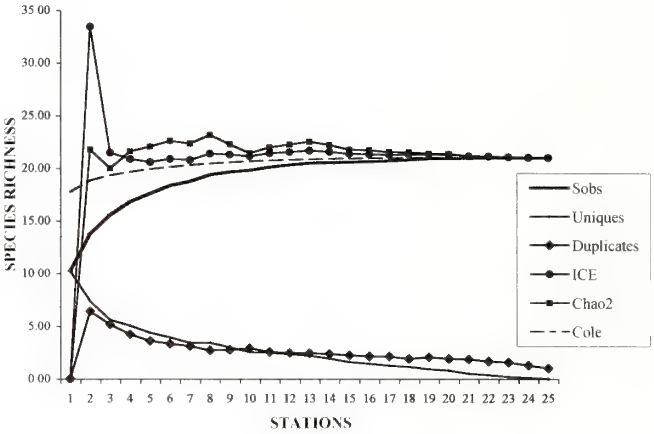

Figure 2. Species richness estimators and patchiness indicators for the micro-snails of the Yungas in Tucumán. Species accumulation curves and Coleman curves obtained with EstimateS 5.0.1.

Other diversity indices used in this work were the Shannon Index, Evenness Index and the Whittaker Index. The Shannon Index (H′) determines the alpha (α) diversity obtained through the equation:

$$H' = -\sum p_i \log_2 p_i$$

Where p_i= proportion of individuals in the i^{th} species (ni/N) (Magurrán 1989). Evenness (E) was calculated using the formula:

$$E = H'/H_{\max}$$

Its value fluctuated between 0 and 1. An E=1 means that all of the species present at the station are equally abundant (Magurrán 1989). To estimate beta (ß) diversity we used the Whittaker index (*I*):

$$I = (S/\alpha) - 1$$

which consist of the total number of species (S) divided by the mean number of species per station (α) (Whittaker 1975, Magurran 1989, de Winter and Gittenberger 1998). The Whittaker index provides a measurement of the variability among sites (= stations). The community that contributes with fewer species will have the highest β diversity. If *I* is equal to 1, then the stations have the same or identical faunas and higher values indicate increasing differentiation (de Winter and Gittemberg 1998). The Whittaker index does not take into account the distribution of species on spatial or environmental gradients, so this index is not intended to be used to measure species turnover (Vellend 2001). The total number of specimens recovered per station (each station of 100 m^2) was used as an estimate of abundance.

RESULTS

Faunal composition

In the present study, we found 7741 specimens representing 21 species in 15 genera and 9 families, one of them was a "prosobranch" and the remaining were pulmonates (Table 2). The total species per stations data matrix is given in Table 3. The most speciose family was Charopidae, with a total of seven species recorded. Following Charopidae, were Pupillidae (3 species) and Systrophiidae (3 species). The three families together represented 62% of the total number of species. The rest of the families were represented by lower numbers of species, generally one or two. Of the total number of families represented, only one is carnivorous, the rest are herbivorous or detritivorous. The species richness per station ranged from 4 to 14 species (Table 1). The richest stations, with 14 species recorded, were between 1000 m and 1200 m of elevation in the San Javier mountains (Tables 1, 3). These stations were located in the biological reserve of the National University of Tucumán, a protected area called Parque Sierra de San Javier.

Density fluctuated between 16 and 809 specimens per 100 m^2 (Table 3). The densest station was Potrero de Las Tablas with 809 specimens in 100 m^2 located at 750 m. Abundance of specimens was low in those stations that had a substrate with sand, or with a high proportion of small stones and that were more exposed to sunlight. The most common and abundant taxa were *Adelopoma tucma* Doering, 1884 and *Wayampia trochilioneides* (d'Orbigny, 1835). Some species of the genus *Radiodiscus* Pilsbry, 1906 were also very abundant, especially in stations from San Javier Mountain (Tables 1, 3). The micro-molluscan fauna was dominated by two families, Systrophiidae and Diplommatinidae, that were present in 24 out of 25 stations sampled, although the number of genera represented in each of these families was low in the study region. Individuals of *W. trochilioneides* were absent only in stations 10 and 17 corresponding to San Miguel de Tucumán city and Medinas (Tables 1, 3). Station 10 had an environment modified by human activities, where invasive species (*Zonitoides arboreous* [Say, 1816], *Opeas pumilum* [Pfeiffer, 1840]) were more frequent than native ones. Station 17 was a dry transition forest habitat with a low frequency of occurrence of several species that typically inhabit humid forests. Individuals of *A. tucma* were very abundant in humid habitats of low montane forest, especially when those habitats were well preserved, as at stations 1-4. When the conditions of the forests

Table 2. Systematic classification of the species collected at the 25 stations sampled in the Yungas of Tucumán. Classification systems according to Wade *et al.* (2001) and Muller da Fonseca and Thome (1993).

CLASS GASTROPODA
SUBCLASS PULMONATA
ORDER EUPULMONATA
  SUBORDER STYLOMMATOPHORA
  INFRAORDER ORTHURETHRA
  FAMILY PUPILLIDAE
    Pupisoma latens Hylton Scott, 1960
    Pupisoma dioscoricola (Adams, 1845)
    Gastrocopta pulvinata Hylton Scott, 1948
  INFRAORDER SIGMURETHRA
  FAMILY CHAROPIDAE
    SUBFAMILY ROTADISCINAE
      Radioconus pilsbryi (Hylton Scott, 1957)
      Radioconus crenulatus (Hylton Scott, 1963)
      Radiodiscus wygodzinskyi Weyrauch, 1965
      Radiodiscus katiae Hylton Scott, 1948
      Radiodiscus golbachi Weyrauch, 1965
      Trochogyra gorduraensis (Thiele, 1927)
    SUBFAMILY AMPHIDOXINAE
      Ptychodon amancaezensis (Hidalgo, 1869)
  FAMILY HELICODISCIDAE
      Lilloiconcha tucumana (Hylton Scott, 1963)
  FAMILY FERUSACCIIDAE
    Caecilioides consobrina (d'Orbigny, 1835)
  FAMILY SYSTROPHIIDAE
    Wayampia trochilioneides (d'Orbigny, 1835)
    Drepanostomella tucma Hylton Scott, 1948
    Miradiscops sp.
  FAMILY ZONITIDAE
    Zonitoides arboreus (Say, 1916)
    Zonitoides nitidus (Müller, 1774)
  FAMILY EUCONULIDAE
    Guppya lilloana Hylton Scott, 1948
    Guppya aenea Hylton Scott, 1948
  FAMILY SUBULINIDAE
    Opeas pumilum (Pfeiffer, 1840)
SUBCLASS "PROSOBRANCHIA"
ORDER CAENOGASTROPODA
  SUBORDER ARCHITAENIOGLOSSA
SUPERFAMILY CYCLOPHOROIDEA
  FAMILY DIPLOMMATINIDAE
    Adelopoma tucma Doering, 1884

showed some alteration or had secondary vegetation, *A. tucma* was notably less common or was completely absent. The species *Guppya aenea* (Hylton Scott, 1948) had a high frequency of occurrence (96%) in the stations, being absent only in Medinas (station 17), but the congeneric *Guppya lilloana* (Hylton Scott, 1948) occurred with less frequency (84%). Among the less frequently occurring taxa was *Lilloiconcha tucumana* Hylton Scott, 1963 (12%) found only in piedmont forest and in low montane forest of San Javier. It was absent in all the other locations. *Opeas pumilum* (Pfeiffer, 1840), *Z. arboreous* and *Zonitoides nitidus* (Müller, 1774) were found in localities with high human activities, such as Tucumán City, Villa Nougues, and El Cadillal stations.

Table 3. Data matrix of the species collected and the stations sampled and used in the analysis.

SPECIES/ STATIONS	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Radioconus pilsbryi	0	1	0	16	14	0	0	0	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0
Radiodiscus crenulatus	2	0	3	2	11	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	10	8	3
Radiodiscus wygodzinskyi	55	86	240	146	0	1	0	37	4	0	3	30	9	0	14	0	0	19	0	0	0	0	0	0	4
Trochogyra gorduraensis	8	1	79	16	0	18	0	0	18	0	0	1	0	0	0	4	6	0	0	0	0	0	14	2	4
Ptychodon amancaezensis	1	6	5	2	0	28	5	0	0	0	1	0	6	6	0	0	7	4	88	138	4	0	30	40	2
Radiodiscus golbachi	0	0	0	2	0	0	0	0	1	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Lilloiconcha tucumana	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Radiodiscus katiae	20	15	13	16	5	4	0	0	0	0	3	10	26	0	6	0	0	0	189	139	5	14	40	35	0
Cecilioides consobrina	7	13	0	0	0	0	4	17	0	0	9	55	30	5	8	0	0	0	0	0	0	10	37	11	0
Zonitoides arboreus	1	0	0	0	0	0	13	0	0	1	0	44	0	11	0	1	113	0	0	0	0	0	0	0	0
Zonitoides nitidus	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pupisoma latens	7	5	5	2	0	1	1	3	11	0	1	12	14	0	2	1	0	0	19	31	0	14	52	31	15
Pupisoma dioscoricola	0	0	0	0	0	0	0	0	0	0	0	0	14	0	5	0	0	13	0	0	0	3	19	0	0
Gastrocopta pulvinata	0	0	0	0	0	0	0	5	0	0	9	6	7	0	0	0	0	0	12	11	0	2	1	33	0
Wayampia trochilioneides	104	46	105	31	9	57	42	249	25	0	67	55	92	63	26	29	0	146	102	288	5	5	50	67	63
Miradiscops sp.	32	70	26	21	5	20	28	31	10	0	21	9	0	1	3	0	0	0	4	9	0	8	16	10	52
Dreponostomella tucma	1	2	2	6	0	20	3	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0
Guppya lilloana	10	2	18	5	4	23	2	10	8	0	1	11	50	10	6	0	0	1	4	8	1	8	8	8	0
Guppya aenea	27	12	60	20	3	35	4	34	32	11	9	31	109	42	4	3	0	27	25	27	1	14	40	55	2
Adelopoma tucma	290	29	131	101	0	4	67	420	6	15	146	87	2	0	74	16	0	35	0	34	0	10	364	191	105
Opeas pumilium	0	0	0	0	0	0	2	0	0	55	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
TOTAL	565	289	688	386	51	211	173	809	115	82	270	352	362	138	148	55	141	245	445	687	16	88	681	491	253
Mean number of specimens per station	27	14	33	18	2.4	10	8.2	39	5.4	3.9	13	17	17	6.5	7	2.6	6.7	12	21	33	0.7	4.1	32	23	12

Table 4. Calculated values of the Shannon index (H′), Whittaker index (*I*), and Evenness for each sampled station.

STATIONS	H′	*I*	Evenness
1	2.3097	0.50	0.6066
2	2.7856	0.50	0.7316
3	2.6649	0.50	0.7202
4	2.6817	0.50	0.7043
5	2.6163	2.00	0.932
6	2.9126	0.90	0.8419
7	2.4355	0.75	0.704
8	1.883	0.90	0.5668
9	2.7591	1.33	0.8704
10	1.175	4.25	0.7413
11	2.3091	0.90	0.6441
12	3.0736	0.61	0.8306
13	2.7911	0.75	0.7786
14	2.0256	2.00	0.7215
15	2.3689	1.10	0.7131
16	1.8242	2.00	0.6498
17	1.0877	4.25	0.5044
18	1.8369	2.00	0.6543
19	2.1997	1.30	0.6939
20	2.334	1.10	0.7026
21	2.0488	3.20	0.8824
22	3.1332	1.10	0.9432
23	2.5152	0.61	0.6797
24	2.8186	0.75	0.7862
25	2.1881	1.10	0.6587

In the altitudinal transect between 800 and 1460 m of elevation in the San Javier Mountains, the species richness and composition of the micro-snail community between piedmont and low montane forest were the same. A sharp decrease in the number of species (from 14 to 7) was detected between low montane and upper montane forest. Density was also low in the upper montane forest.

Diversity estimators and diversity index

The behavior of ICE and Chao2 estimators with respect to the accumulation species curve (Sobs) is shown in Fig. 2. The gap between richness estimators and the observed species accumulation curve was very narrow. The curves converged, becoming flat with increasing numbers of samples. Both Chao2 and ICE estimators estimated 21 species, which closely approximated the observed species accumulation curve at the sample number 20. The behavior of the "rare" species curves (uniques and duplicates) was typical of a complete inventory (Heyer *et al.* 1999). When the number of stations was low the curve for the unique species rose faster than did the curve for duplicate species. With increasing numbers of stations, both declined, crossing and tending towards zero when no species remained to be discovered and almost all species were known from two or more localities. In the present analysis the calculated Coleman curve nearly followed the observed curve, showing no evidence of patchiness.

The diversity values obtained using the Shannon index fluctuated from 1.08-3.13 (Table 4). The most diverse stations were in the Escaba area (H′ = 3.13; E = 0.94) (station 22) and El Cadillal (H′ = 3.07; E = 0.83) (station 12). The stations with lowest diversities were Medinas (H′ = 1; E = 0.50) (station 17) and San Miguel de Tucumán city (H′ = 1.17; E = 0.74) (station 10).

The values calculated for the Evenness Index (E) ranged from 0.56 to 0.94 (Table 4). These high values close to 1 mean that those stations were not very different in species abundance. The stations richest in species (stations 2-4, each with 14 species recorded) had similar high values of evenness (0.70-0.73), meaning that in each of these stations the species were close to be equally abundant.

The Whittaker index (*I*) fluctuated between 0.50 and 4.25 with an average of 1.46 (Table 4). This high value indicated a substantial degree of beta diversity or differentiation among stations.

DISCUSSION

We recorded the presence of 21 species of micromolluscs from stations in the Yungas area in northwestern Argentina. Comparisons of species richness with previous works worldwide are difficult to make because most of them had considered macro- and micro-molluscs together and applied different methodologies. Some of the studies carried out in the southern hemisphere reported the highest levels of species richness in the world. Barker and Mayhill (1999) reported the presence of 105 species of terrestrial molluscs within the Pukeamaru District in New Zealand, de Winter and Gittenberger (1998) reported 97 species of land snails in a square kilometer of rainforest in Cameroon and in Madagascan rainforests, 80 species of micromolluscs in 20 × 20 m patches were found by Emberton *et al.* (1996), and 61 species were found in a square kilometer in Malaysian Borneo (Schilthuizen and Rutjes 2001). The North American land snail fauna is relatively well studied (Lydeard *et al.* 2004). Emberton (1995) reported that the most diverse site is located on Pine Mountain, Kentucky, U.S.A., which has yielded 44 species of land gastropods in four hectares. In Central and South America, several lists of taxa from restricted geographical localities are available in some countries but research on diversity of land gastropods are very scarce. In consequence, diversity is probably seriously underestimated. In Mexico, a total of 52 species have been reported from tropical rain forest leaf litter in southern Veracruz (Naranjo-García 1997), 34 species from a km^2 of forest in French Guyana (Gargominy and Ripken 1998), and in the Camisea region, Perú, 49 species have been also found (Ramírez *et al.* 1999). Unfortunately, countries like Bolivia or Colombia with a high biodiversity have been poorly inventoried for land snails.

Although the species richness recorded for Tucumán in the present study is low (21 species of micro-snails) in comparison with other previously studied sites in the southern hemisphere, the total number of specimens collected was very high (7741 micro-molluscs specimens). Density in our study (specimens in a 10 × 10m station) ranged from 16 to 809 and varied altitudinally. In comparison, Emberton *et al.* (1999), working in southeast areas (total of 0.04 ha) of Madagascar, found a total of 2430 specimens from 80 micromolluscan species. Densities (specimens in a 20 × 20 m plot) in their study ranged from 20 to 104. In the present study, species richness and density declined with increasing altitude along a transect carried out in San Javier Mountains. The highest density in Tucumán was found in Potrero de Las Tablas, a piedmont forest station.

The most speciose family of the micro-mollusc fauna in Tucumán is Charopidae with 7 species represented in the area from a total of 26 species of the same family reported for Argentina (Fernández 1973). Charopidae is the dominant and most speciose family of other faunas of the southern hemisphere, such as the Pukeamaru fauna in New Zealand. Barker and Mayhill (1999) found 56 species of Charopidae in that area, a notably higher species richness compared to Tucumán. One of the dominant families in our study was Systrophiidae, with three species represented in Tucumán out of 8 species of this family reported for Argentina (Fernández 1973). In northern areas of South America, the Systrophiidae were found to be one of the predominant families, as is the case in Camisea, Perú, with 14 species reported in that study area (Ramirez *et al.* 1999) from a total of 55 species cited for the whole country (Ramirez *et al.* 2003). On the contrary, the family Charopidae (25 species reported for Argentina [Fernández 1973]) seems to be more abundant in southern South America than in Perú (13 species reported [Ramírez *et al.* 2003]). Studies on distribution, species richness, and systematic classification of Charopidae from South America are still scarce. Many families that are common and abundant in northern South America are not present or are poorly represented in southern South America. Similarly, another carnivorous family, the Streptaxidae, which is very abundant and diverse in northern South America, is scarce in southern areas of South America.

Adelopoma tucma Doering, 1884, one of the most common species in the Yungas, was very abundant in the richest stations of this study, with specimens numbers ranging from 105 to 420 in stations with 10 to 14 species (the highest species number recorded in a station). This species is very abundant in well preserved forests between 600 and 1200 m of elevation that had low human impact. This species was less common or is completely absent in places where the substratum and vegetation were altered by human activity. This was apparent in stations 1-4 from the San Javier protected area that has a low human impact compared with the other stations. A second highly abundant species was *Wayampa trochilioneides* (d'Orbigny, 1835), whose number of specimens was high at the same stations as *A. tucma.* In areas of piedmont forest with anthropogenic alterations, some non-indigenous species from the genera *Opeas* Albers, 1860 and *Zonitoides* Lehmann, 1862 were present. Of the indigenous fauna, the less frequently found species were *Lilloiconcha tucumana* Hylton Scott, 1963 (Helicodiscidae), which was found in only two stations, and *Radiodiscus golbachi* Weyrauch, 1965 (Charopidae), found in three stations. On the contrary, the most frequently found species of the indigenous fauna was *Guppya aenea* (Hylton Scott, 1948), which was found in 24 stations.

According to our study, the inventory was found to be complete by the non-parametric estimators of diversity used, which are particularly suitable for small samples (Colwell and Coddington 1994). These results indicated that with further collecting effort in this area no other species would probably be found. Historical records for Tucumán province, mainly from malacological collections, show the presence of additional species of micromolluscs, such as *Zilchogyra hyltonscottae* Weyrauch, 1965 and *Radiodiscus thomei* Weyrauch, 1965 (Charopidae). These two species were not found in our study area, perhaps because species of Charopidae inhabiting South America are not well described. Taxonomic revisions are urgently needed, in part to test the validity of nominal species. For instance, *Radiodiscus thomei* Weyrauch, 1965 and *Radiodiscus katiae* Hylton Scott, 1948, are extremely similar and original descriptions do not provide unique characters for each species. A revision of the genus is necessary to resolve these taxonomic issues.

The Coleman curve closely followed the observed species-accumulation curve, indicating that aggregation in the data was not affecting estimates of species richness. The true diversity of micro-snails in the Yungas of Tucumán was estimated to be 21 species, with a high abundance of specimens.

The β diversity calculated with the Whittaker index had a high mean value of 1.46. This suggests substantial differentiation in species composition among the stations (Barker and Mayhill 1999). The richest stations, such as those in San Javier (1-4 in Fig. 1, Table 1) had similar Whittaker indices (0.5), but station 5 from the upper montane forest of San Javier that had a low species richness, had a high value of the Whittaker index (2), meaning that there was difference in diversity of the fauna present in this last station in comparison with the others. Stations with high Whittaker indices, have low species richness (Magurrán 1989) and, in this case, were the ones with more human pressure (*e.g.*, stations 10, 17).

The α diversity, the diversity in each station/community, calculated with the Shannon index, showed the highest values at El Cadillal (station 12) and Escaba (station 22). These values were similar to the ones obtained in some stations of the Pukeamaru area in New Zealand (Barker and Mayhill 1999). However, values obtained with the Shannon index are difficult to compare with other places because of the different methodology employed and area considered.

Land snail faunas of tropical rainforest tend to be quite diverse (Emberton *et al.* 1996). Much of this diversity is a consequence of the micro-molluscan fauna. Because most South American rainforests are largely undercollected for micro-land snails and are undergoing significant deforestation, there is an urgent need to collect and study the molluscan fauna. In solving the present biodiversity crisis, taxonomic work remains an essential tool. Revisionary taxonomy is frequently dismissed as merely descriptive, which belies its strong intellectual content and hypothesis-driven nature (Wheeler 2004). Diversity studies on South American molluscan fauna as well as systematic revisions of land molluscs are urgently needed and must be developed, especially in countries where high biodiversity occurs.

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Out of Australia: *Belloliva* (Neogastropoda: Olividae) in the Coral Sea and New Caledonia

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Abstract: The genus *Belloliva* (Gastropoda: Olividae) consists of small (<15 mm) operculate species and was hitherto thought to be essentially confined to coastal waters of southern and eastern Australia. We report a small radiation from deep water (100-1000 m) in the Coral Sea and New Caledonia, consisting essentially of undescribed species. The new genus *Calyptoliva*, which differs from *Belloliva* by the absence of a mantle filament and the presence of a mantle lobe, is also represented in the same area by new species. Based on correlation with shell characters, we suggest that the olivid mantle lobe is responsible for secreting the primary spire callus that overlies the suture, rather than producing the columellar callus as was previously believed (Marcus and Marcus 1959). *Belloliva* and *Calyptoliva* combine a suite of shell, radular, and anatomical characters that is shared with either the Olivinae or the Ancillariinae. This raises the question of the distinctiveness of the two classically recognized subfamilies within the family Olividae. All species have paucispiral protoconchs with inferred limited larval dispersal, and many have extremely narrow distributions, sometimes endemic to a single guyot, or they show discrete geographical differentiation. New species: *Belloliva iota* sp. nov., *Belloliva alaos* sp. nov., *Belloliva apoma* sp. nov., *Belloliva ellenae* sp. nov., *Belloliva obeon* sp. nov., *Belloliva dorcas* sp. nov., *Calyptoliva bolis* gen. nov., sp. nov., *Calyptoliva amblys* sp. nov., *Calyptoliva tatyanae* sp. nov.

Key words: Anatomy, classification, new species, endemism

The neogastropod family Olividae stands out as a minor component in offshore and deep-water molluscan faunas. Only 15 species have been recorded worldwide from depths below 400 m, all belonging to subfamily Ancillariinae (Kantor and Bouchet 1999), with only four of these (belonging to genera *Amalda, Ancilla*, and *Baryspira*) reaching below 1000 m. Ongoing exploration of deep-water benthos in the South West Pacific confirms this unspectacular diversification of Olividae in the local molluscan fauna (Kilburn and Bouchet 1988, Bouchet and Kilburn 1991), although species of *Amalda* can be locally common on seamounts of the Norfolk Ridge (Y. Kantor and P. Bouchet pers. obs.). The discrete radiation of species from the Coral Sea and New Caledonia described in the present paper is thus remarkable because of its magnitude: 11 species, 8 of which reach or normally occur below 400 meters, and all of them undescribed. Six species are placed in the genus *Belloliva* Iredale in Peile, 1922, and three in the new genus *Calyptoliva*.

The genus *Belloliva* Iredale in Peile, 1922 was established for *Olivella brazieri* Angas, 1877, and a second species from Australian coastal waters, *Olivella pardalis* A. Adams and Angas, 1864, was also originally included in the genus. Peile (1922: 18) highlighted that the two species "have a tricuspid rachidian, similar to that of *Oliva* but with minute additional cusp outside each of the lateral cusps;" this was the basis for the establishment of *Belloliva*. Since Peile (1922), no anatomical data nor additional data on radulae have been published, and the genus has remained little known. Based on radular morphology, Olsson (1956) allocated *Belloliva* to the subfamily Olivinae, whereas Wilson (1994) without any discussion included the genus in the subfamily Olivellinae, an opinion that was followed by Tursch and Greifeneder (2001). Currently, *Belloliva* includes four Australian coastal species; a fifth one from the Caribbean has also controversially been referred to it (see Discussion below).

In the present paper, we redefine *Belloliva* based on the anatomy of the Australian species, including the type species; we describe the Coral Sea and New Caledonian species attributable to it; we describe the new genus *Calyptoliva* that superficially resembles *Belloliva*; and finally we discuss the position of *Belloliva* in the family Olividae.

MATERIAL AND METHODS

The present paper is based on the extensive material collected by recent expeditions exploring the Coral Sea and New Caledonia area (Richer de Forges 1990, 1993, Richer de Forges and Chevillon 1996) and housed in Muséum national d'Histoire naturelle, Paris (MNHN). The material is not individually catalogued but is unambiguously referred to by the acronym of the cruise (e.g., MUSORSTOM 4, BATHUS

1) and the station number. In lists of material examined, "lv" refers to live-taken specimens and "dd" to empty shells.

The following standard shell measurements were made: shell length (SL); last whorl length (BWL); aperture length (AL); shell width (SW). For the purposes of species discrimination, we used a number of protoconch and teleoconch measurements following those defined and described in detail by Tursch and Germain (1985, 1986), and demonstrated by us to be operational (Bouchet and Kantor 2004). The method used for counting protoconch whorls or measuring protoconch is usually not specified in the literature, making comparisons difficult. We counted protoconch whorls from the origin of the suture (Fig. 1B). The number of protoconch and teleoconch whorls was counted with an accuracy of 0.125 whorl.

Because measurements taken from camera lucida drawings are more accurate than those made directly on the shell with the aid of an ocular micrometer, protoconchs were drawn in standard position, i.e., with the protoconch-teleoconch transition facing the observer (Fig. 1), and measurements were made from the drawings. Instead of protoconch diameter, we used "D1" which equals protoconch diameter + 0.25 of the first teleoconch whorl. "PRE" represents the exposed height of the protoconch and is referred to in the text as protoconch elevation. "TL1" is the diameter of the first 1.25 teleoconch whorls (this measurement can easily be done on the drawings of "standard" protoconch position). Measurements "TL2" and "TL3" are defined on Fig. 1A.

Radulae were studied with scanning electron microscopy (SEM). After being cleaned in diluted bleach, air-dried, mounted on glass slides, and coated with gold-palladium they were investigated with a JEOL JSM 840A Scanning Microscope.

We studied histology of some organs of *Belloliva* (anterior foregut and mantle). The tissues were dehydrated and embedded in paraffin and serially sectioned at 10 μm. Sections were stained with Masson's triple stain.

The terminology of the shell base of oliviform gastropods has not yet been fully standardized and is sometimes "taxonomy-dependent" (e.g., "ancillid band" and "ancillid groove"). We follow Tursch and Greifeneder (2001), who discussed the terminology used in descriptions of olivid genera and suggested homologies. The shell base of *Belloliva* is rather simplified in comparison with other olivid genera. The anterior band (Fig. 2B) is usually covered with inconspicuous axial striations. It is elevated over the surface of the remaining part of the last whorl (cloak, Fig. 2A) and delimited by a rather sharp step (sometimes referred to as "groove," or "ancillid groove": see Kilburn 1977). The plication plate (Fig. 2C) in turn is raised over both the cloak and the anterior band. It can be divided (by the posterior limit of the anterior band, or ancillid groove) into parietal plate and anterior plating. The parietal plate is a slightly thickened area, actually formed by the parietal callus. Its surface can differ from the cloak, being very finely shagreened. The anterior plating is sharply delimited from the anterior band on the ventral shell surface, but this border becomes more obscured on the lowest part of the shell. The plication plate can be smooth, but usually has several plicae on the anterior plating and a few on the parietal plate.

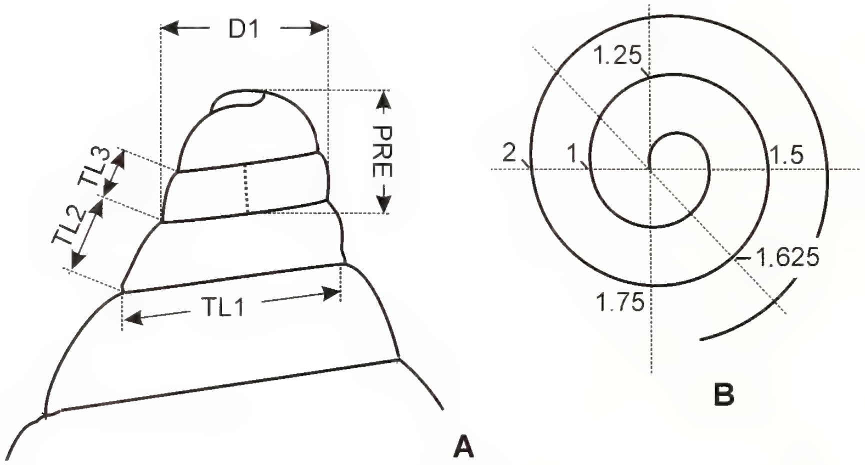

Figure 1. Standard orientation of protoconch and measurements made. A, Shell in the standard position with protoconch-teleoconch transition marked by dotted line; measurements taken on protoconch: D1, PRE; measurements taken on teleoconch: TL1 to TL3 (see Material and Methods for description and references). B, Count of whorl number.

RESULTS

Olividae Latreille, 1825
Belloliva Iredale in Peile, 1922

Type species

Olivella brazieri Angas, 1877 (original designation).

Remarks

Four Australian species have traditionally been included in *Belloliva* (Kaicher 1987, Wilson 1994) (for more details see Discussion). Here we describe in details the anatomy of the type species, *Belloliva brazieri*, and provide comparative remarks on the second studied Australian species, *Belloliva leucozona*.

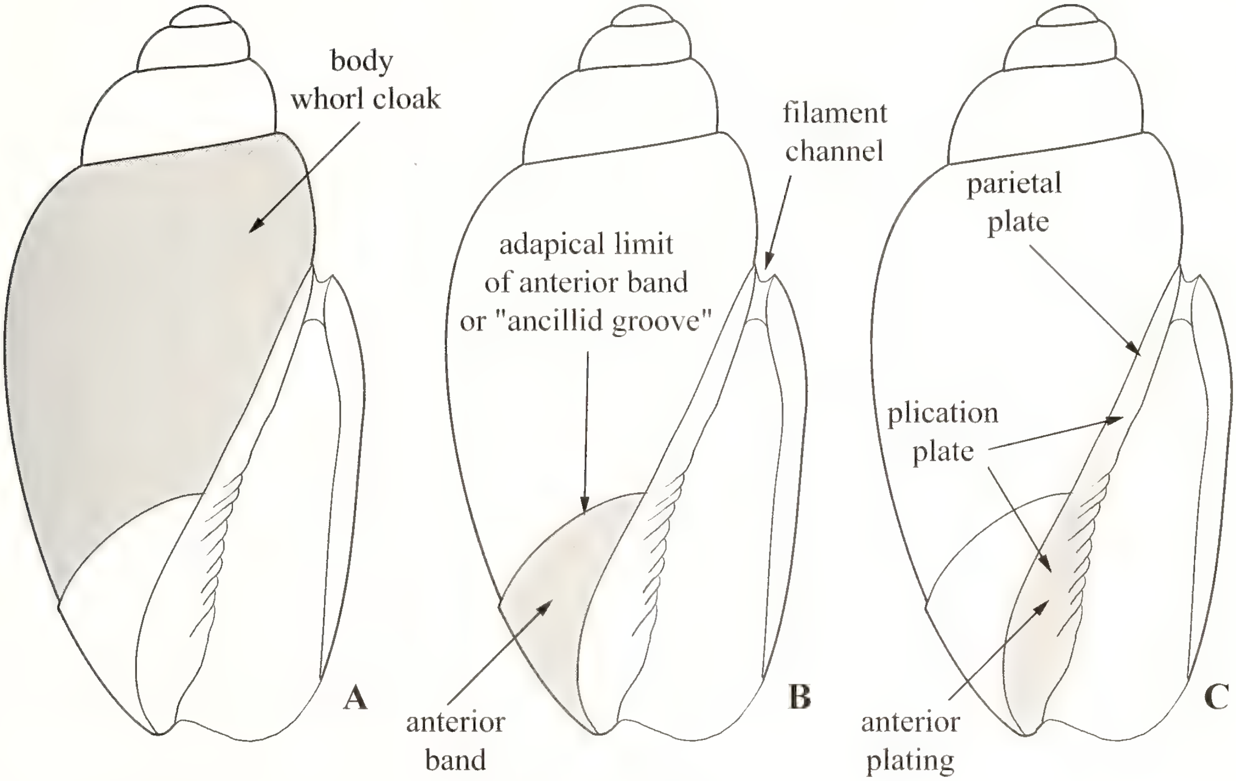

Figure 2. Terminology used in shell descriptions, with emphasis on the shell base.

Belloliva brazieri (Angas, 1877)
(Figs. 3, 4A-D, 32A-B)

Olivella brazieri Angas 1877: 172, pl. 26, fig. 6.

Type material

Not traced.

Type locality

Newcastle Beach, New South Wales, Australia.

Material examined

Australia, New South Wales, 2 km E of Long Bay, Sydney, 33°58.8′S, 151°17.0′E, 66 m, AMS C388726. Dissected specimen male: SL 12.9, BWL 9.75, AL 7.4 mm, SW 4.8 mm. After dissection, the radula was removed and the anterior foregut was serially sectioned.

Anatomy

General morphology.—Body consisting of nearly 5 whorls, mantle cavity spanning about 0.5 whorl, nephridium more than 0.3 whorls, digestive gland about 1.25 whorls, testis about 3 upper whorls (Fig. 3A-B). Nephridium with transparent walls, excretory lamellae very distinct in posterior part and more closely spaced anteriorly, 15 in total. Nephridial gland narrow. Anterior lobe of digestive gland small, spanning about 0.3 whorls and separated from posterior lobe by the stomach, which is oriented obliquely with regard to columellar axis (Fig. 3A). Posterior lobe spanning slightly less than one whorl, occupying the entire width of the whorl immediately posterior to the stomach and more posteriorly has the shape of narrow band occupying the upper part of the whorl above testis. Foot thick, metapodium broadly triangular-oval, propodium small in comparison with crescent shaped propodium typical for Olividae, subdivided longitudinally on the ventral surface (Fig. 3C) and separated from metapodium by thin but distinct furrow on both the dorsal and ventral sides. Parapodia of medium size. Operculum completely transparent, yellowish, very thin, elongate-oval. Operculum attached along narrow oval area (about 0.5 of operculum width) to opercular pad. In its posterior third, part of the opercular pad is free from the dorsal side of the foot, forming a tongue-like projection. Head rather large, with two separate vertical flaps (Fig. 3C, tn) separated by a long, deep furrow. No eyes.

Mantle cavity (Fig. 3F).—Mantle edge even and slightly thickened. Mantle thin, osphradium, ctenidium, and hypobranchial gland visible by transparency. Siphon with thick and contracted walls, long, extending considerably beyond

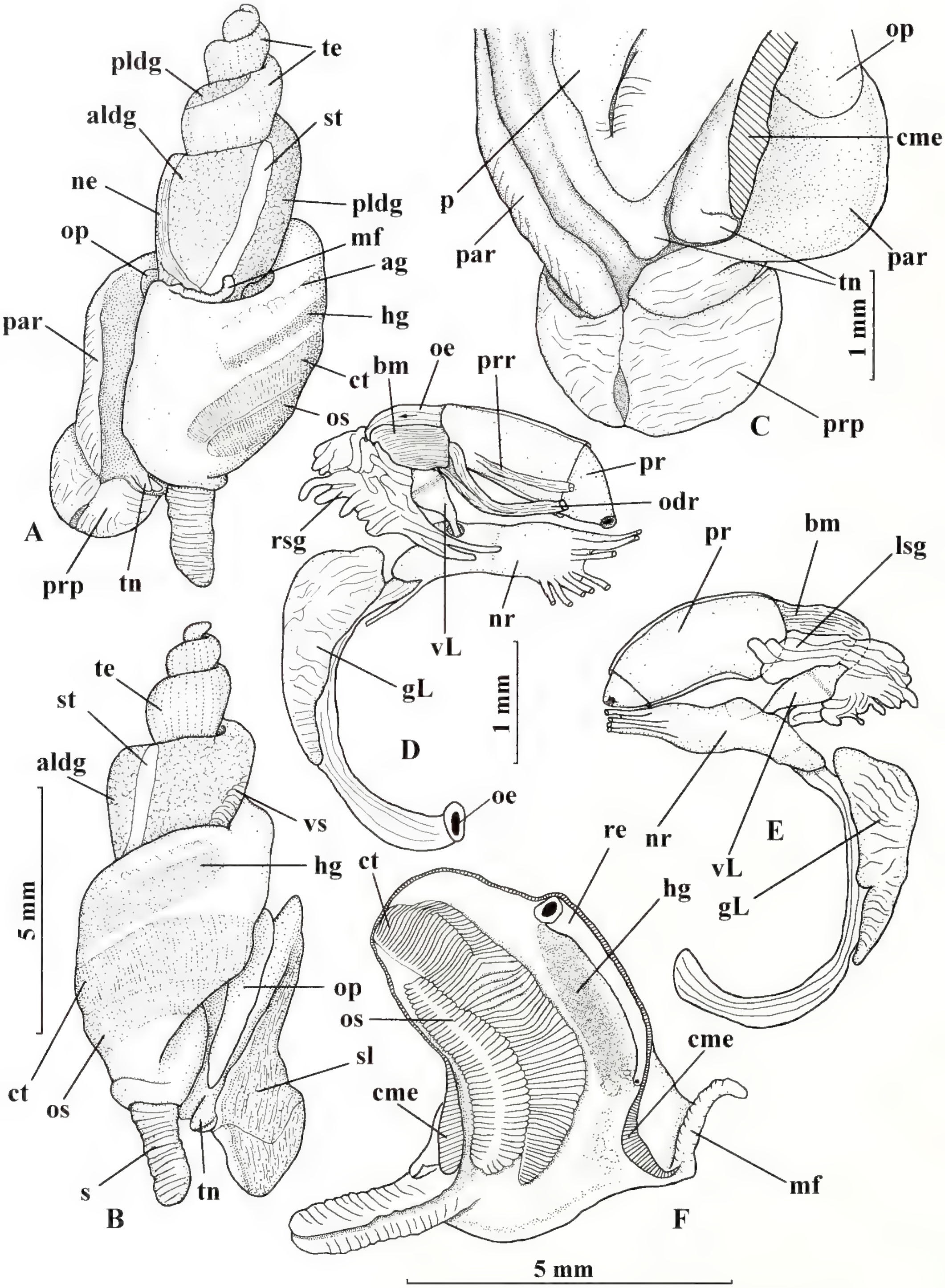
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Figure 3. Anatomy of *Belloliva brazieri* (Angas, 1877). A, B, Dorsal and ventral views, respectively, of the body removed from the shell. C, Head-foot, antero-dorsal view, mantle removed. D, E, Right and left views, respectively, of the anterior foregut. F, Mantle complex. Abbreviations: ag, anal (rectal) gland; aldg, anterior lobe of digestive gland; bm, buccal mass; cme, cut mantle edge; ct, ctenidium; gL, gland of Leiblein; hg, hypobranchial gland; lsg, left salivary gland; mf, mantle filament; ne, nephridium; nr, circumesophageal nerve ring; odr, odontophoral retractor; oe, esophagus; op, operculum; os, osphradium; p, penis; par, parapodium; pldg, posterior lobe of digestive gland; pr, proboscis; prp, propodium; prr, proboscis retractor; re, rectum; rsg, right salivary gland; s, siphon; sl, sole of the foot; st, stomach; te, testis; tn, cephalic tentacles; vL, valve of Leiblein; vs, seminal vesicle.

mantle edge. Ctenidium large, occupying about 0.8 of mantle length, consisting of simple triangular lamellae. Osphradium as wide as ctenidium and 0.75 of its length, symmetrical. Mantle filament (Fig. 3A, F, mf), rather short when contracted. Mantle lobe and anterior mantle tentacles absent. Hypobranchial gland very distinct, narrow, brown, lacking folds. Rectum narrow, very thin in posterior third, gradually narrowing towards the anal opening. Rectal gland distinctly visible through the mantle wall as a narrow red sinuose line (Fig. 3A, ag), extending along most of rectum length.

Alimentary system (Fig. 3D-E).—Rhynchostome asymmetrical, situated below the right head flap. Proboscis short in contracted state (1.4 mm, or 0.19 AL), occupying nearly the entire rhynchocoel length, rhynchodeum semitransparent. Proboscis walls and rhynchodeum very thin, about 30 µm (7% of proboscis diameter), covered by cuticularized cuboidal epithelium in histological section. Walls with a very thin outer layer of circular muscle fibers and an inner layer of longitudinal fibers, constituting about half of the wall thickness. Mouth opening very broad compared to proboscis diameter. Buccal tube long (about 0.3 of proboscis length) and broad, lined with thick cuticle, leading to buccal cavity. Radular diverticulum long and narrow, extending at least 0.5 of proboscis length. Odontophoral retractor large, flattened (Fig. 3D, odr), extending posteriorly from the proboscis, running anteriorly along ventral side of rhynchodeum and bypassing the nerve ring, following to the ventral side of cephalic hemocoel, its edges thickened, the muscle itself being rather thin and transparent. Esophagus rather broad posterior to proboscis and forming a very short loop. Several very thin retractor muscles attached to the rhynchodeum (wall of the proboscis sheath) in its mid-length. Odontophore protruding significantly behind the proboscis edge. Radular sac nearly as long as odontophore. Radula (Fig. 4A-D) comprising about 80 teeth rows, membrane width about 120 µm (0.93% SL, 1.62% AL). Rachidian tooth with 3 main cusps, central cusp about 1.5 times narrower and shorter than the lateral cusps, and an additional small but distinct cusp abutting each side of the main lateral cusps. Small and shallow depressions on dorsal side of main lateral cusps, corresponding to cusps of preceding row. Anterior profile of the rachidian slightly concave. Lateral sides of basal plate gradually embedded into the membrane without distinct border. Lateral teeth (Fig. 4D) with subrectangular base and long, curved, hook-like cusp. Valve of Leiblein large, pyriform, well demarcated from the esophagus, with ciliary cone. Esophagus very narrow immediately posterior to the valve and passing through the nerve ring. Circumesophageal nerve ring comparatively very large, nearly as long as retracted proboscis. Posterior esophagus (posterior to the opening of the duct of the gland of Leiblein) significantly widening as approaching the stomach. Gland of Leiblein large, colorless in preserved condition, bulky anteriorly, and tapering posteriorly, opening into esophagus by very short and constricted duct close to the nerve ring. Gland of Leiblein with broad internal cavity, separated by tall and rather narrow folds. Salivary glands medium-sized, separate, loose, ramified-tubular, typical for Olivoidea (Fig. 3D-E, rsg, lsg). Wall of each tube composed of a single layer of large, irregularly angular, glandular cells with granulated cytoplasm, at least some of them ciliated. Glands situated on both sides of posterior part of rhynchodeum and anterior esophagus and tightly attached to them by connective tissue fibers. Salivary ducts rather thick, passing into the tubules of the salivary glands without obvious border. Ducts fused with the walls of esophagus at posterior end of proboscis. Accessory salivary glands absent. Stomach badly damaged while extracting the body, but in general appearance similar to that of *Belloliva leucozona* (see below).

Reproductive system.—Testis large, occupying 3 upper whorls, situated ventral to the digestive gland in the anterior part, contrary to other neogastropods. Seminal vesicle poorly differentiated from the testis, consisting of few loops and situated at the lower part of the whorl, in close proximity to the stomach. Within the mantle cavity, seminal duct and prostate gland forming several large tight loops and then extending to the base of the penis. Penis as long as the mantle cavity, of even diameter along its length, tip rounded, without seminal papilla.

Belloliva leucozona (A. Adams and Angas, 1864)
(Figs. 4E-H, 5, 32C-D)

Olivella leucozona A. Adams and Angas 1864: 422, pl. 37, fig. 23.

Type material

Four syntypes BMNH 1870.10.26.93.

Type locality

Port Jackson, New South Wales, Australia, 6 fathoms (11 m).

Material examined

Australia, New South Wales, 2.3 km E of Malabar, 33°59.5′S, 151°16.8′E, 66-73 m, AMS C330373. Dissected specimen, male: SL 12.25, BWL 8.89, AL 7.13, SW 4.38; after dissection, mantle serially sectioned.

Anatomy

Body morphology (Fig. 5A-B) is similar to that of *Belloliva brazieri*, except that testis spans 3.5 whorls instead of 3 in *B. brazieri*. Nephridium has less pronounced excretory lamellae, 9 in total as seen through nephridial wall.

Mantle cavity.—Mantle cavity in all details similar to that of *Belloliva brazieri*. The main difference is the absence

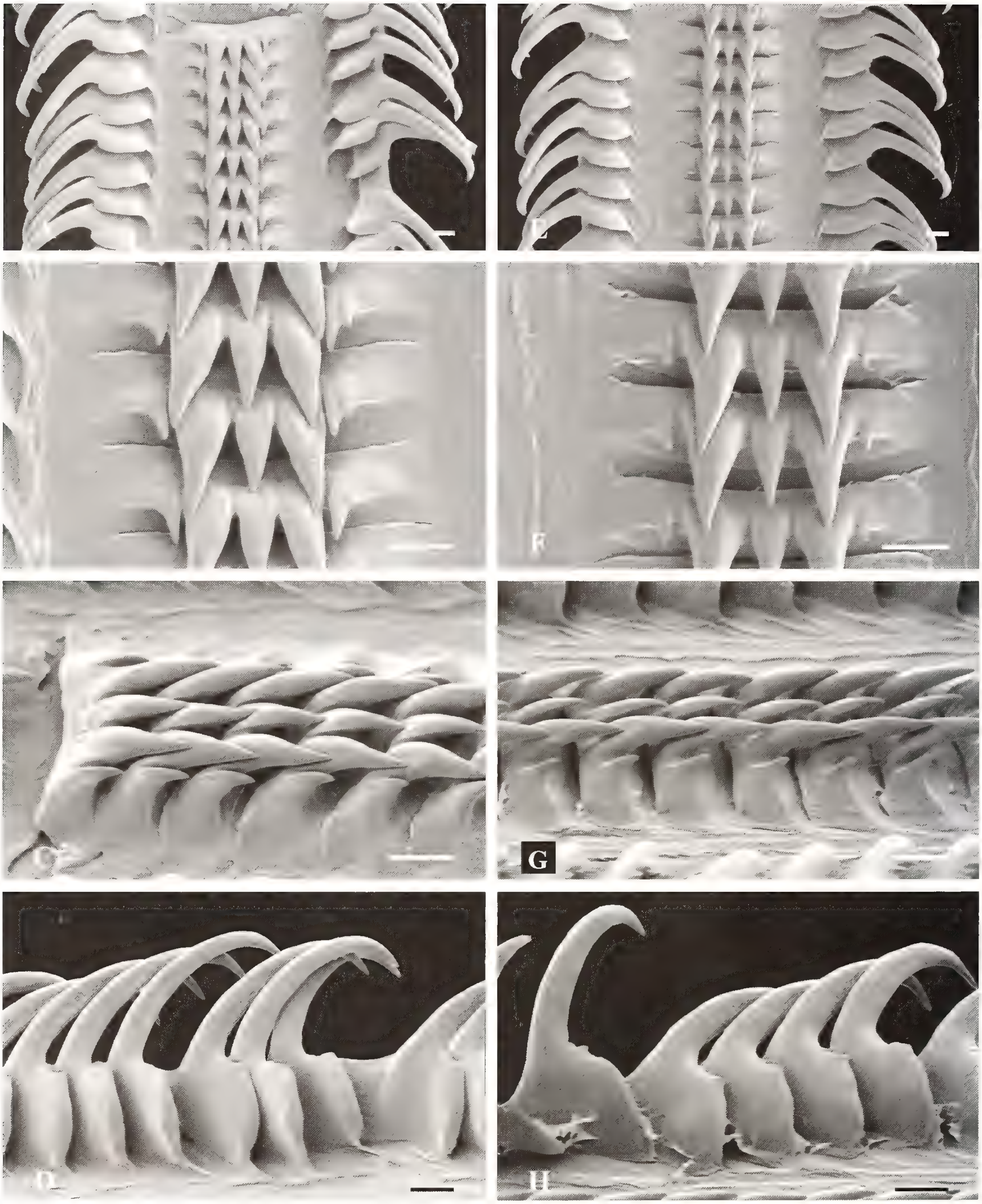

Figure 4. Scanning electron micrographs of the radulae of *Belloliva brazieri* (A-D) and *Belloliva leucozona* (E-H). A, E, Dorsal view of the central part of the radular membrane. B, F, Enlarged rachidian teeth. C, G, Left lateral view of the rachidian teeth. D, H, Left lateral view of the lateral teeth. Scale bars = 10 μm.

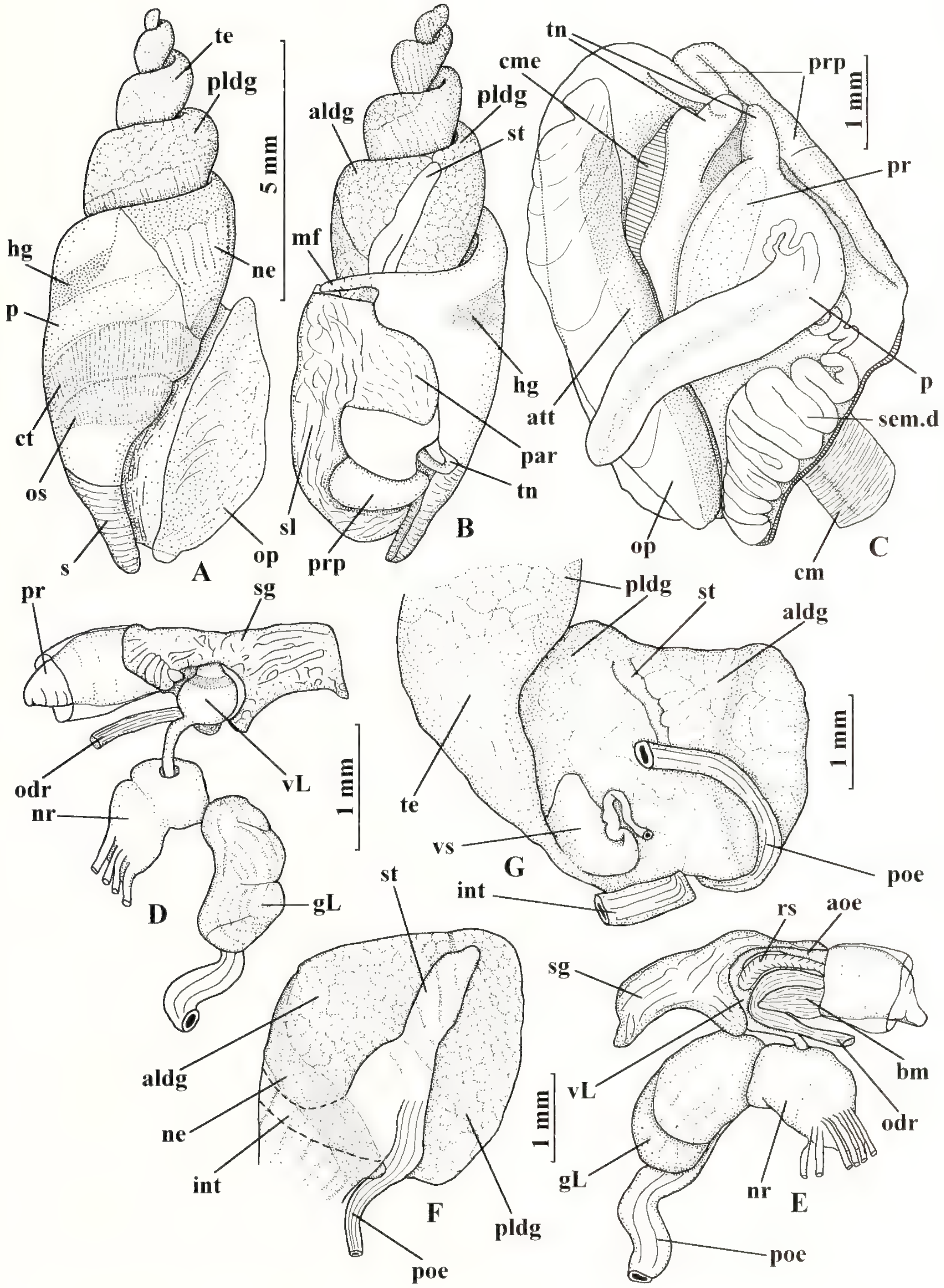

Figure 5. Anatomy of *Belloliva leucozona* (A. Adams and Angas, 1864). A, B, Ventral and dorsal views, respectively, of the body removed from the shell. C, Head-foot, dorsal view, mantle and visceral mass removed. D, E, Left and right views, respectively, of the anterior foregut. F, External view of the stomach and part of the visceral mass. G, Posterior whorl of the visceral mass, view from inside, whorls slightly uncoiled, nephridium removed. Abbreviations: aldg, anterior lobe of digestive gland; aoe, anterior esophagus; att, attachment of the opercular pad to the operculum; bm, buccal mass; cm, columellar muscle; cme, cut mantle edge; ct, ctenidium; gL, gland of Leiblein; hg, hypobranchial gland; int, intestine; mf, mantle filament; ne, nephridium; nr, circumesophageal nerve ring; odr, odontophoral retractor; op, operculum; os, osphradium; p, penis; par, parapodium; pldg, posterior lobe of digestive gland; poe, posterior esophagus; pr, proboscis; prp, propodium; rs, radular sac; s, siphon; sem.d, seminal duct; sg, salivary gland; sl, sole of the foot; st, stomach; te, testis; tn, cephalic tentacles; vL, valve of Leiblein; vs, seminal vesicle.

of the rectal gland. Filament channel on upper shell whorls occluded with solid debris and obviously filament is not able to extend further than about last 2.5 whorls. Mantle filament (serially sectioned) composed mostly of muscular elements, both longitudinal and helical, with few connective tissue cells. Innervation poor.

Alimentary system.—Anatomy of the alimentary system is similar to *Belloliva brazieri*. The minor differences include: shorter proboscis in contracted state (0.85 mm, or 0.12 AL) (Fig. 5D, E, pr); odontophore and radular sac strongly protruding posterior to the proboscis (Fig. 5E, bm, rs); radular sac slightly longer than odontophore; relatively larger and more rounded valve of Leiblein (Fig. 5D, vL); position of the valve more anterior to the circumesophageal nerve ring; larger fused salivary glands (Fig. 5D, E, sg), situated posteriorly to the retracted proboscis and surrounding anterior esophagus and valve of Leiblein; more coiled gland of Leiblein (Fig. 5D, E, gL).

Radula (Fig. 4E-H) comprised of about 80 teeth rows, membrane width about 130 μm (1.1% SL, 1.82% AL). Anterior profile of rachidian straight.

Reproductive system. Seminal vesicle situated at the ventral border between gonad and posterior lobe of digestive gland, comprising a very thickened, wide, short vesicle, and the much narrower duct (Fig. 5G, vs). Seminal duct entering the mantle cavity where it forms numerous very wide loops on the right side of the mantle cavity and continuing to the base of the penis (Fig. 5C, sem.d), nearly straight within penis.

Belloliva alaos Kantor and Bouchet sp. nov.
(Figs. 6, 7, 8A-C, 9)

Type material

Holotype (Moll 9469) and 4 paratypes (Moll 9470) in MNHN.

Material examined

North of New Caledonia. MUSORSTOM 4, st. DW156, 18°54′S, 163°19′E, 525 m (2 dd); st. DW159, 18°46′S,

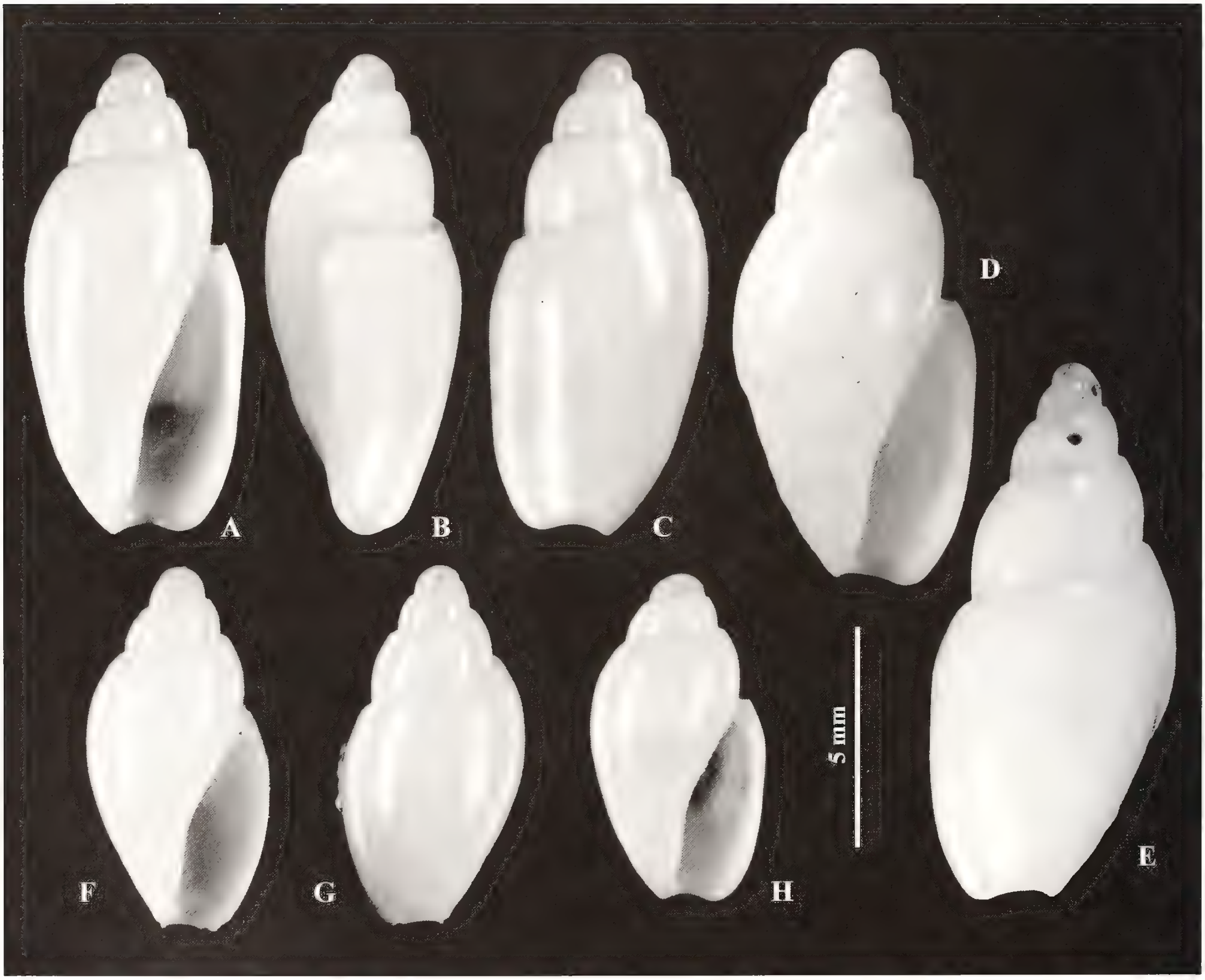

Figure 6. *Belloliva alaos* sp. nov. A-C, Holotype. D, E, Paratype (st. DW918, SL 12.1 mm). F, G, Paratype (st. DW918, SL 8.2 mm). H, St. DW916, SL 7.2 mm. All shells illustrated at the same scale.

163°16′E, 585 m (11 dd); st. DW160, 18°42′S, 163°13′E, 668 m (5 dd, 1 lv [anatomy and radula]). BATHUS 4, st. DW914, 18°49′S, 163°15′E, 600-616 m (1 dd); st. DW916, 18°53′S, 163°20′E, 518-570 m (1 dd); st. DW917, 18°47′S, 163°14′E, 397-400 m (27 dd); st. DW918, 18°49′S, 163°16′E, 613-647 m (22 dd—holotype and 4 paratypes); st. DW919, 18°50′S, 163°17′E, 610-660 m (1 dd).

Type locality

North of New Caledonia, 18°49′S, 163°16′E, 613-647 m (BATHUS 4, st. DW918).

Description (holotype)

Shell solid, glossy, oval (BWL/SL = 0.76, AL/SL = 0.60, D/SL = 0.46), with moderately wide aperture and elevated, somewhat turreted spire, consisting of about 1.0 protoconch and almost 3 teleoconch whorls. Protoconch large, evenly rounded, diameter 1650 µm, exposed height 1140 µm, smooth, protoconch-teleoconch transition distinctly marked by onset of filament channel. Profile of whorls evenly rounded, with very obtuse shoulder. Filament channel completely open. Aperture lanceolate-oval, gradually narrowing abapically. Outer lip slightly convex, nearly straight in most adapical part, straight in middle portion and evenly rounded abapically. Parietal plate narrow, slightly thickened, anterior plating having one inconspicuous plica. Color uniformly white, upper teleoconch whorls and protoconch translucent.

Dimensions (holotype): SL 10.8 mm, SW 5.0 mm, BWL 8.2 mm, AL 6.5 mm. Largest specimen (paratype): SL 12.1 mm, SW 5.3 mm, BWL 8.6 mm, AL 6.5 mm.

Anatomy

The anatomy of the single live-taken female (SL 11.7 mm, BWL 9.6 mm, AL 7.5 mm, SW 6.0 mm) has been studied (Fig. 7). Body in alcohol uniformly pale yellow, lacking pigmentation.

General morphology.—Body consisting of nearly 4 whorls, mantle cavity spanning about 0.5 whorls, nephridium 0.3 whorls, digestive gland about 1 whorl. Ovary occupying upper 2 whorls of the visceral hump, its border with posterior digestive gland forming a wavy line across the whorl. Nephridium with transparent walls, with 8 main excretory lamellae (Fig. 7B, ne). Nephridial gland narrow, with nearly smooth walls (Fig. 7B, ng). Anterior digestive gland small, spanning about 0.25 whorls and completely separated from posterior one by obliquely situated stomach (Fig. 7A, C). Foot thick, strongly contracted during fixation, folded transversely, metapodium broadly triangular-oval, propodium small in comparison to metapodium, typically crescent-shaped, subdivided longitudinally (Fig. 7C). Operculum transparent, very thin, elongate, constricted in adapical part, and slightly thickened along low inner edge. Operculum attached to opercular pad along long narrow area (less than 0.3 of operculum width) (Fig. 7B, att). About 1/5 of most posterior part of the pad detached from dorsal surface of the foot, forming a tongue-like extension. Head weakly distinguished from the body, with two separate small vertical flaps (Fig. 7C, tn). No eyes.

Mantle cavity.—Mantle edge even. Mantle thin, and osphradium and ctenidium are seen through it. Siphon short, rather thin-walled, slightly extending beyond mantle edge, with smooth edges. Osphradium bipectinate, nearly symmetrical, with very narrow axis, very broad, slightly exceeding the maximal width of large, deeply pendant ctenidium (Fig. 7G, os). The inner row of osphradial lamellae overhang the ctenidium; when viewing the mantle from the inside, the osphradial maximal width appears to be 1.5 the ctenidial width. The length of osphradium nearly equals the length of ctenidium. Ctenidium occupies nearly entire mantle length, formed of very tall triangular lamellae. Hypobranchial gland moderately glandular, although not forming distinct folds (Fig. 7G, hg). Mantle filament not long, with folded walls, indicating significant state of contraction. Posterior mantle tentacle and mantle lobe absent. Female pallial gonoduct large, swollen. *Bursa copulatrix* rather large, long, subcylindrical. Female genital opening situated close to anus.

Alimentary system.—Rhynchostome asymmetrical, situated below the right tentacle. Proboscis short in contracted state (about 1.7 mm, or 0.3 AL) (Fig. 7D, E, pr), thin (about 0.5 mm in diameter), occupying nearly the entire rhynchocoel length. Rhynchodeum (Fig. 7E, rnh) thin-walled, semitransparent. Proboscis wall very thin, about 20 µm (4% of the proboscis diameter), lined with low cuboidal epithelium (12 µm), underlain by single layers of circular and longitudinal muscle fibers (8 µm thick overall). Mouth opening rather wide. Muscular buccal tube, not less than 0.5 of proboscis length, leading from mouth to buccal cavity. Wall of buccal tube, in contrast to proboscis wall, thick, about 130 µm in total, lined with thick cuticle (20 µm) and cubical epithelium (12 µm), and underlain by very thick layer of circular muscles (about 90 µm). Proboscis lumen filled with oval cells with slightly granular cytoplasm. Several very thin retractor muscles attached to median part of rhynchodeum (wall of the proboscis sheath) when proboscis is retracted. From posterior to the proboscis, esophagus rather narrow and forming a long loop when proboscis is retracted. Large odontophoral retractor leaving proboscis from the posterior, extending anteriorly along ventral side of rhynchodeum and bypassing the nerve ring, attached to ventral side of cephalic hemocoel (Fig. 7E, odr). Radula (Fig. 8A-C) about 145 µm wide (1.24% SL, 1.93% AL), consisting of 70 rows of teeth. Rachidian with 3 main cusps, central cusp having the same width as the lateral and about 1.5 times shorter than the lateral cusps, and a secondary, very small, indistinct cusp on

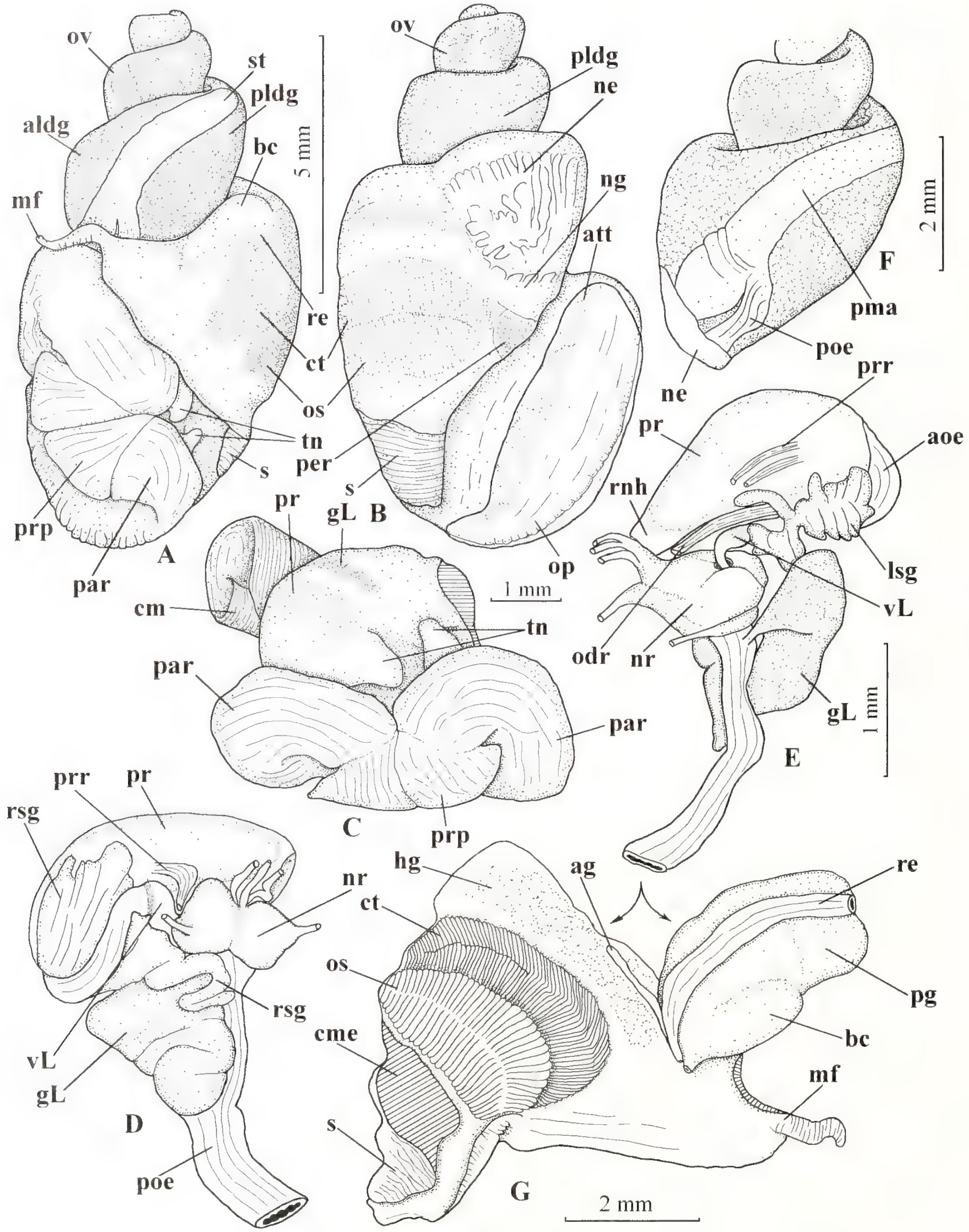
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Figure 7. Anatomy of *Belloliva alaos* sp. nov. A, B, Ventral and dorsal views, respectively, of the body removed from the shell. C, Head-foot, dorsal view, mantle and visceral mass removed. D, E, Right and left views, respectively, of the anterior foregut. F, External view of the stomach and part of the visceral mass. G, Mantle complex. Abbreviations: ag, anal (rectal) gland; aldg, anterior lobe of digestive gland; aoe, anterior esophagus; att, attachment of the opercular pad to the operculum; bc, bursa copulatrix; cm, columellar muscle; cme, cut mantle edge; ct, ctenidium; gL, gland of Leiblein; hg, hypobranchial gland; lsg, left salivary gland; mf, mantle filament; ne, nephridium; ng, nephridial gland; nr, circumesophageal nerve ring; odr, odontophoral retractor; op, operculum; os, osphradium; ov, ovary; par, parapodium; per, pericardium; pg, pallial gonoduct; pldg, posterior lobe of digestive gland; pma, posterior mixing area; poe, posterior esophagus; pr, proboscis; prp, propodium; prr, proboscis retractor; re, rectum; rnh, rhynchodeum (=proboscis sheath); rsg, right salivary gland; s, siphon; st, stomach; tn, cephalic tentacles; vL, valve of Leiblein.

each side of the main lateral cusps; secondary cusps most visible on lateral view of the rachidians (Fig. 8C, indicated by black arrows). Rachidians rather widely spaced, cusps not abutting the next teeth. Anterior profile of the rachidian slightly convex, nearly straight. Lateral sides of the basal plate gradually embedded in the membrane without distinct border. Lateral teeth with subtriangular bases and long, curved, hook-like cusps. Valve of Leiblein large, pyriform, well distinguished from esophagus, which becomes very narrow immediately after the valve and passes through the nerve ring. Circumesophageal nerve ring comparatively very large, with enlarged pedal and buccal ganglia. Posterior esophagus significantly widening posteriorly towards the stomach. Gland of Leiblein large, very light brown, tubular, and coiled, bulky anteriorly, opening into esophagus by very narrow constricted duct abutting the nerve ring posteriorly. Salivary glands medium-sized, ramified-tubular, left one slightly smaller than right, situated on either side of esophagus and nearly fused around valve of Leiblein, in retracted position of proboscis situated mostly on right side of rhynchodeum, rather loose in appearance with several blind tubules extending from the main part of the gland. Salivary ducts poorly differentiated from the glands, appearing like short extensions of the tubules. They enter the esophageal wall anterior to the valve of Leiblein and pass towards their openings the lateral folds of esophagus. Accessory salivary glands absent. Stomach large, with very long posterior mixing area (Fig. 7F, pma) that spans more than 0.5 whorl. Stomach anatomy not investigated due to poor fixation. Rectal gland a simple, blind, rather long tube (Fig. 7G, ag), colorless.

Distribution

North of New Caledonia, shells in 400-668 m, alive in 668 m.

Remarks

Belloliva alaos sp. nov. is conchologically most similar to *Belloliva apoma* sp. nov., and they could easily be mistaken as variations of one another unless their anatomy is examined. However, *B. alaos* is distinguished by its significantly larger adult size, 12.1 versus 7.6 mm, and its slightly larger protoconch (Fig. 9). Anatomically, *B. alaos* is readily distinguished by the presence of a large operculum and the absence of eyes. The radulae also differ markedly in the shape of the rachidian: in *B. alaos*, the basal plate of the rachidian is shorter than in *B. apoma* and the anterior profile is nearly straight; in *B. apoma*, the basal plate is longer and the anterior profile, which coincides with the anterior edge of the basal plate, is clearly convex. In addition, in *B. apoma* the central cusp is relatively much narrower and shorter than in *B. alaos*.

Etymology

From the Greek *alaos*, blind.

Belloliva apoma Kantor and Bouchet sp.nov.

(Figs. 8D-F, 9, 10)

Type material

Holotype (Moll 9471) and 3 paratypes (Moll 9472) in MNHN.

Material examined

North of New Caledonia. BATHUS 4, st. DW923, 18°52′S, 163°24′E, 470-502 m (15 dd) (co-occurring with *Belloliva exquisita* and *Belloliva simplex*); st. DW929, 18°52′S, 163°23′E, 502-516 m (7 dd, 2 lv [holotype with dried soft parts and 3 paratypes]). LAGON, st. 475, 18°36′S, 163°11′E, 415-460 m (16 dd). MUSORSTOM 4, st. DW197, 18°51′S, 163°21′E, 550 m (1 dd).

Type locality

North of New Caledonia, 18°52′S, 163°23′E, 502-516 m (BATHUS 4, st. DW929).

Description (holotype)

Shell solid, glossy, oval (BWL/SL = 0.80, AL/SL = 0.66, D/SL = 0.51), with moderately narrow aperture and elevated, somewhat turreted spire, consisting of approximately 0.5 protoconch and 2.5 teleoconch whorls. Protoconch large, evenly rounded, diameter 1330 μm, exposed height 770 μm, smooth, protoconch-teleoconch transition distinctly marked by onset of filament channel. Whorls moderately convex, evenly rounded, poorly shouldered. Filament channel completely open. Aperture lanceolate-oval, gradually narrowing adapically. Outer lip rather evenly convex in most adapical part, nearly straight in median part and evenly rounded abapically. Parietal plate narrow, very thin, anterior plating broadening in abapical part of aperture, appearing nearly smooth in front view, but several very weak oblique plicae visible when the shell is slightly rotated clockwise (Fig. 10D). Color uniformly off-white.

Dimensions (holotype): SL 6.8 mm, SW 3.5 mm, BWL 5.4 mm, AL 4.5 mm. Largest specimen (LAGON, st. 475): SL 7.6 mm, SW 3.9 mm, BWL 6.1 mm, AL 5.1 mm.

Eyes large. Operculum absent.

Radular width about 95 μm (1.45% SL, 2.16% AL), consisting of about 55 rows of teeth. Rachidian with 3 main cusps, central cusp more than twice narrower than lateral and about 1.5 times shorter than the lateral cusps, and a very small, indistinct secondary cusp on each side of main lateral cusps (Fig. 8E, F indicated by arrow). Rachidians rather widely spaced, cusps not abutting the next teeth. Anterior profile of the rachidian clearly convex and coinciding with the anterior edge of the basal plate of the tooth. Lateral sides

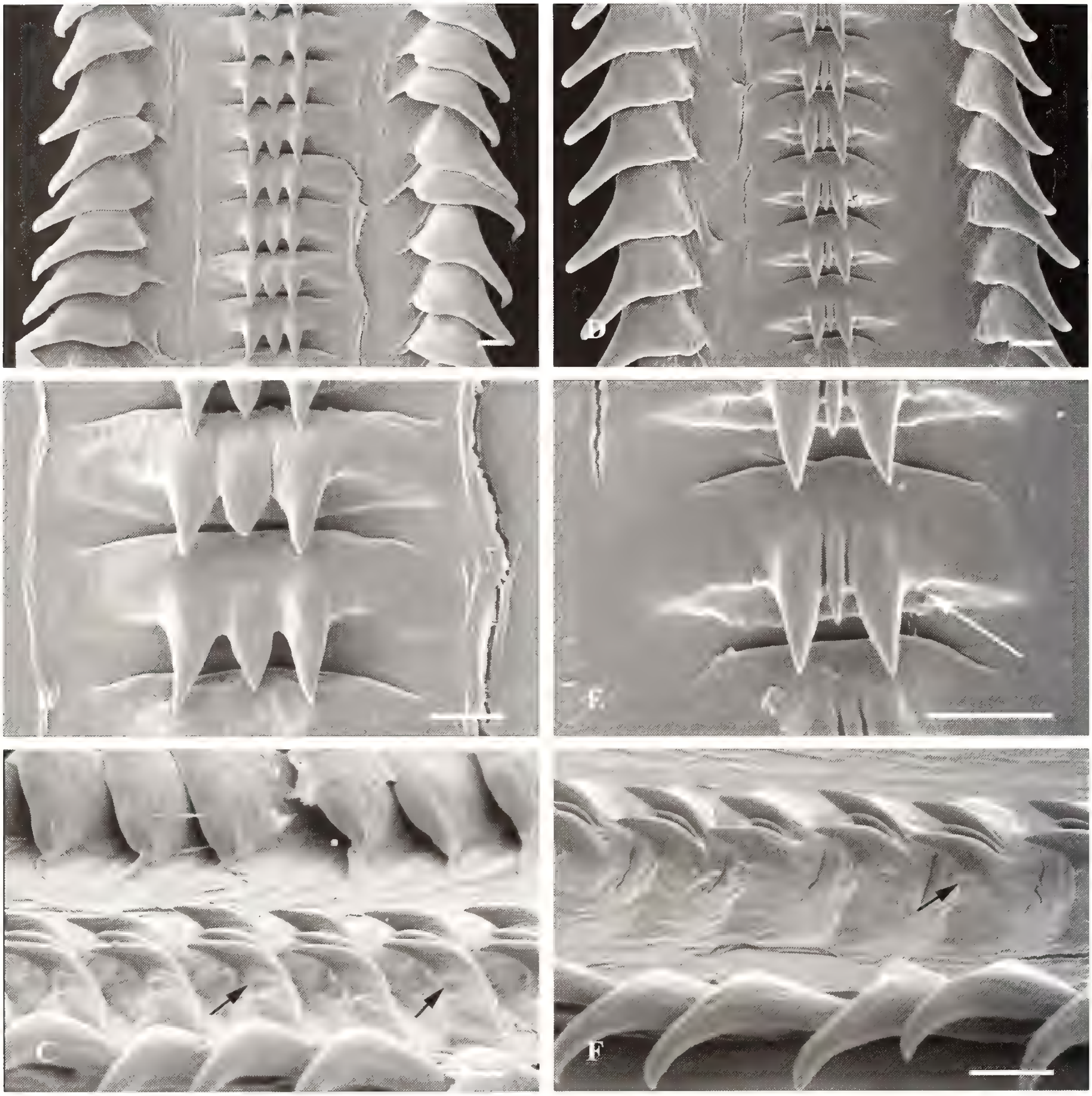


Figure 8. Scanning electron micrographs of the radulae of *Belloliva alaos* sp. nov. (A-C) (MUSORSTOM 4, st. DW160) and *Belloliva apoma* sp. nov. (holotype) (D-F) (BATHUS 4, st. DW929). A, D, Dorsal view of the central portion of the radular ribbon. B, E, Enlarged rachidian tooth. C, F, Left lateral view of the radular ribbon. Arrows on C, E, F indicate secondary cusps of the rachidians. Scale bars = 50 μm (A, D), 10 μm (B, C, E, F).

of the basal plate gradually embedded in the membrane without distinct border. Lateral teeth are with subtriangular bases and long, curved, hook-like cusps.

Distribution

North of New Caledonia, shells in 460-550 m, alive in 502-516 m.

Remarks

Specimens of *Belloliva apoma* may be off-white or may have very faint yellow broad spiral bands (one subsutural and one on shell base above periphery), and/or inconspicuous yellowish-brown spots on the rim bordering the filament channel, and/or also inconspicuous zigzag axial lines on last whorl (Fig. 10H-I).

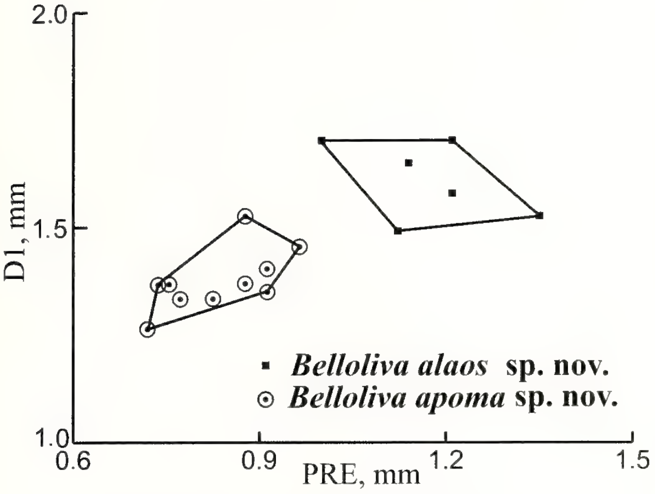


Figure 9. Morphometric comparison of protoconch dimensions of *Belloliva alaos* sp. nov. and *Belloliva apoma* sp. nov.

For comparison with *Belloliva alaos* sp. nov., see under that species.

Etymology

From the Greek *poma*, operculum, and prefix *a*-, without; used as a noun in apposition.

Belloliva simplex (Pease, 1868)
(Figs. 11, 12A-D)

Olivella (Callianax) simplex Pease 1868: 281-282, pl. 23, fig. 24.

Type material

Lectotype designated by Johnson (1994: 24), Academy of Natural Sciences of Philadelphia, ANSP 28969 (Fig. 11A-C).

Material examined

North of New Caledonia. BATHUS 4, st. DW923, 18°52′S, 163°24′E, 470-502 m (1 dd) (co-occurring with *Belloliva exquisita* and *Belloliva apoma*). East coast. LAGON, st. 830, 20°49′S, 165°19′E, 105-110 m (37 dd). BATHUS 1, st. DW692, 20°35′S, 164°59′E, 140-150 m (1 dd). West coast. BATHUS 4, st. DW887, 21°07′S, 164°28′E, 320-344 m (3 dd) (co-occurring with *B. exquisita*). EXPEDITION MONTROUZIER, st. 1255, 20°43′S, 165°08′E, 11 m (3 lv); st. 1259, 20°44.6′S, 165°13.7′E, 15-35 m (2 lv, 4 dd); st. 1260, 20°44′S, 165°14′E, 49-59 m (1 dd); st. 1261, 20°46′-20°47′S, 164°15′-164°16.5′E, 45-65 m (1 lv); st. 1269, 20°35.1′S, 165°08′E, 15-20 m (22 lv, 6 dd); st. 1271, 20°52.7′S, 165°19.5′E, 5-25 m (3 dd); st. 1272, 20°49.5′S, 165°19.6′E, 10 m (10 lv); st. 1273, 20°50.4′S, 165°22.8′E, 20 m (4 dd, 10 lv); st. 1275, 20°49′S, 165°17′E, 50-62 m (2 dd); st. 1311, 20°40.4′S, 164°14.9′E, 10-60 m (9 lv) (co-occurring with *B. exquisita*); st. 1312, 20°40.4′S, 164°14.9′E, 26-40 m (2 dd, 1 lv) (co-occurring with *B. exquisita*); st. 1316, 20°40′S, 164°11.2′E, 12 m (1 lv, 1 dd); st. 1318, 20°41.4′S, 164°14.8′E, 20-30 m (17 lv [radula examined]); st. 1319, 20°44.7′S, 164°15.5′E, 15-20 m (4 lv); st. 1322, 20°45.2′S, 164°15.2′E, 53-71 m (1 dd) (co-occurring with *B. exquisita*); st. 1331, 20°40.6′S, 164°12.1′E, 55-57 m (4 dd) (co-occurring with *B. exquisita*).

Loyalty Islands, Lifou. LIFOU 2000, st. 1423, 20°54.0′S, 167°07.3′E, 12 m (2 dd); st. 1432, 20°53.5′S, 167°02.7′E, 12-32 m (7 dd); st. 1434, 20°52.5′S, 167°08.1′E, 5-20 m (13 dd); st. 1435, 20°55.2′S, 167°00.7′E, 5-30 m (3 dd); st. 1436, 20°55.5′S, 167°04.2′E, 10-20 m (14 dd); st. 1441, 20°46.4′S, 167°02.0′E, 20 m (1 lv, 5 dd); st. 1442, 20°46.4′S, 167°02.0′E, 47 m (1 dd); st. 1443, 20°53.8′S, 167°07.3′E, 48-52 m (3 dd); st. 1454, 20°56.65′S, 167°02.0′E, 15-18 m (1 lv); st. 1456, 20°49.3′S, 167°10.4′E, 25-30 m (7 dd); st. 1469, 20°54.2′S, 167°00.4′E, 70-130 m (1 dd).

Type locality

Paumotus Islands [Tuamotu Archipelago], French Polynesia.

Description

Shell very small, fragile, semitransparent, glossy, oval, with moderately wide aperture and rather low spire, consisting of about 0.75 protoconch and 1.75 teleoconch whorls. Protoconch large in comparison with the teleoconch, evenly rounded, diameter around 1000 µm, smooth, protoconch-teleoconch transition distinctly marked by onset of filament channel. Profile of whorls evenly rounded, last whorl weakly shouldered. Filament channel completely open. Aperture lanceolate-oval, gradually narrowing abapically. Outer lip slightly thickened, almost straight adapically, evenly rounded abapically. Parietal plate narrow, slightly thickened, anterior plating much thicker, broadening on abapical part of aperture, without plicae, clearly concave in profile. Color uniformly off-white.

Dimensions: The lectotype, SL 4.2 mm, seems to be the largest specimen. The largest specimen at our disposal (LAGON, st. 830) has SL 3.8 mm, SW 1.9 mm, BWL 3.1 mm, AL 2.5 mm.

The morphology of one rehydrated female specimen from Koumac, New Caledonia (EXPEDITION MONTROUZIER, st. 1318, SL 4.1, AL 2.5, BWL 3.2, SW 2.0 mm) was examined. Outer morphology similar to other studied species. Eyes large, mantle filament comparatively very short and thick, probably due to fixation. Radula (Fig. 12A-D) about 65 µm wide (1.59% SL, 2.6% AL), consisting of 85 rows of teeth, including 5-6 nascent; width of rachidian approximately 25 µm (38% of radular width). Rachidian narrowly spaced, cusps strongly abutting the next tooth, with

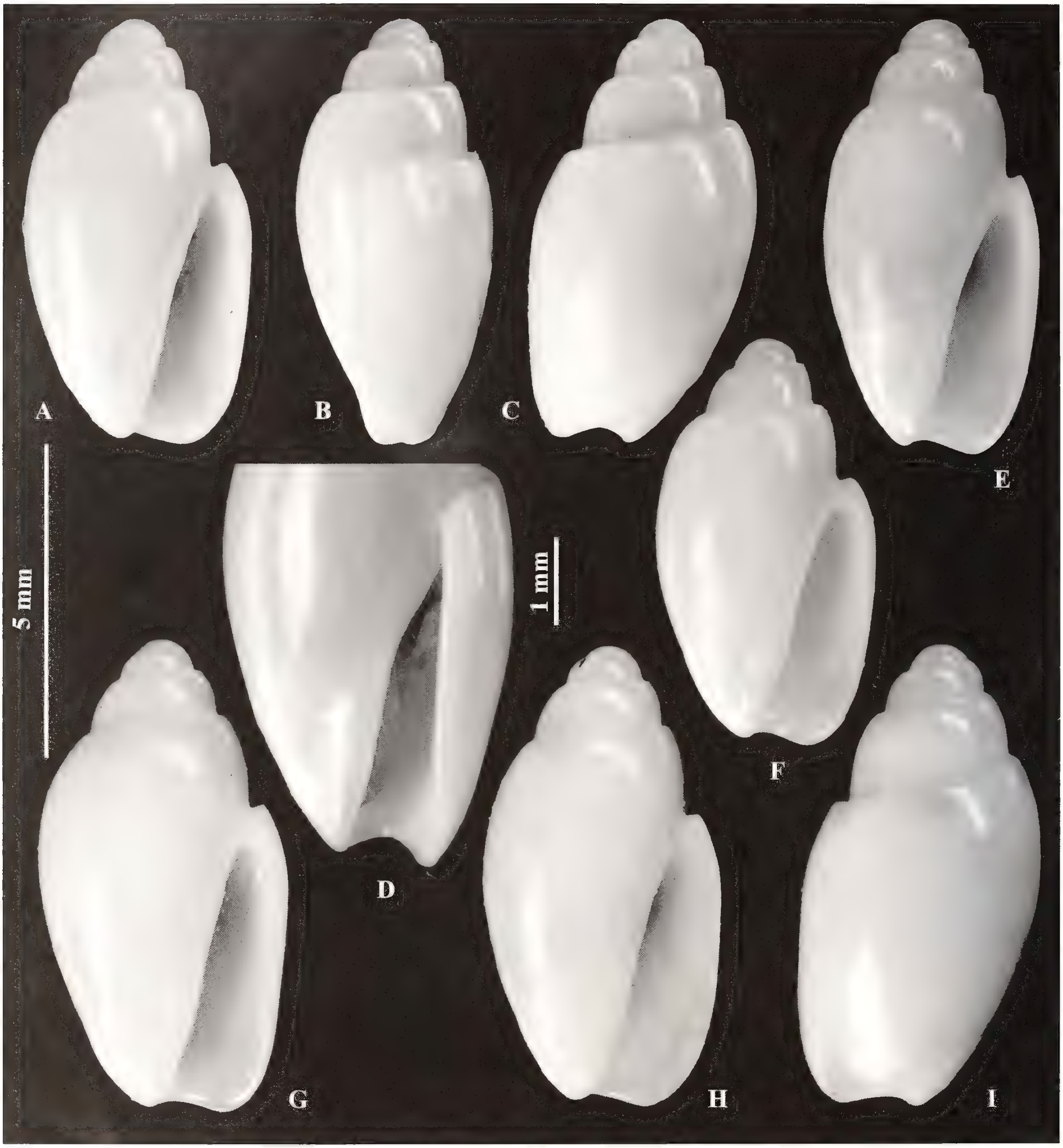


Figure 10. *Belloliva apoma* sp. nov. A-D, Holotype. E, Paratype (SL 7.0 mm). F, Paratype (SL 6.5 mm). G, LAGON, st. 475, SL 7.6 mm. H, I, LAGON, st. 475, SL 7.4 mm. All shells illustrated at the same scale except D.

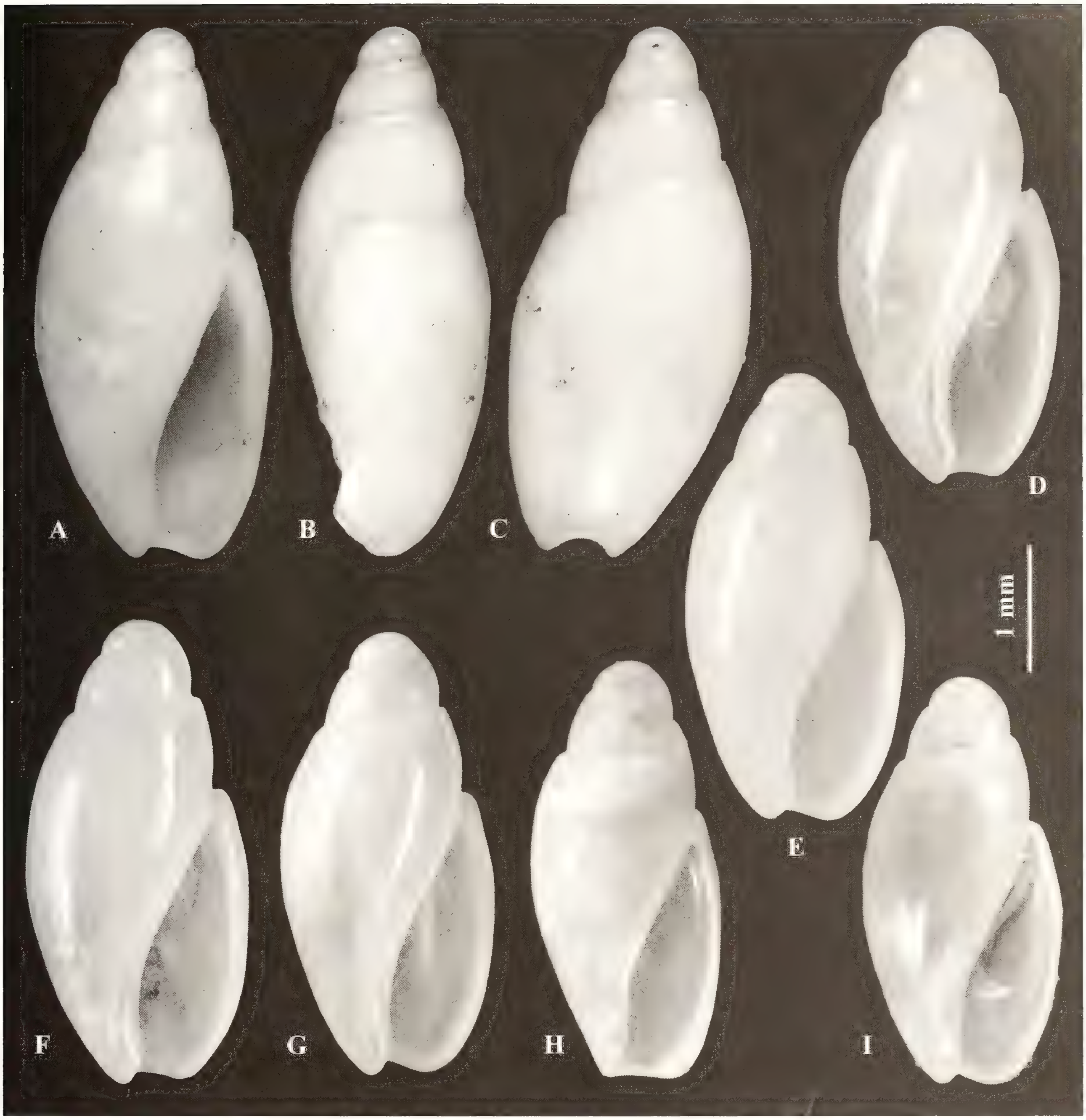


Figure 11. *Belloliva simplex* (Peace, 187X). A-C, Lectotype, ANSP 28969, SL 4.2 mm (courtesy of P. Callomon, ANSP). D-G, New Caledonia, east coast, LAGON, st. 830, 105-110 m. D, (SL 3.6 mm). E, (SL 3.5 mm). F, (SL 3.6 mm). G, (SL 3.5 mm). H, Lifou, st. 1456 m, 25-30 m (SL 3.3 mm). I, New Caledonia, west coast, Expedition Montrouzier, st. 1273, 20 m (SL 3.2 mm). All shells illustrated at the same scale.

short lateral flaps, anterior edge straight, lateral sides of basal plate gradually embedded in membrane without distinct border; 3 main cusps, central cusp narrower and nearly twice as short as the lateral cusps, and a secondary, very small, indistinct cusp on each side of the main lateral cusps; secondary cusps most distinct in lateral view. Lateral teeth with broadened subtriangular bases and long, curved, hook-like cusps, and 2-3 very distinct denticles at the base of the cusp.

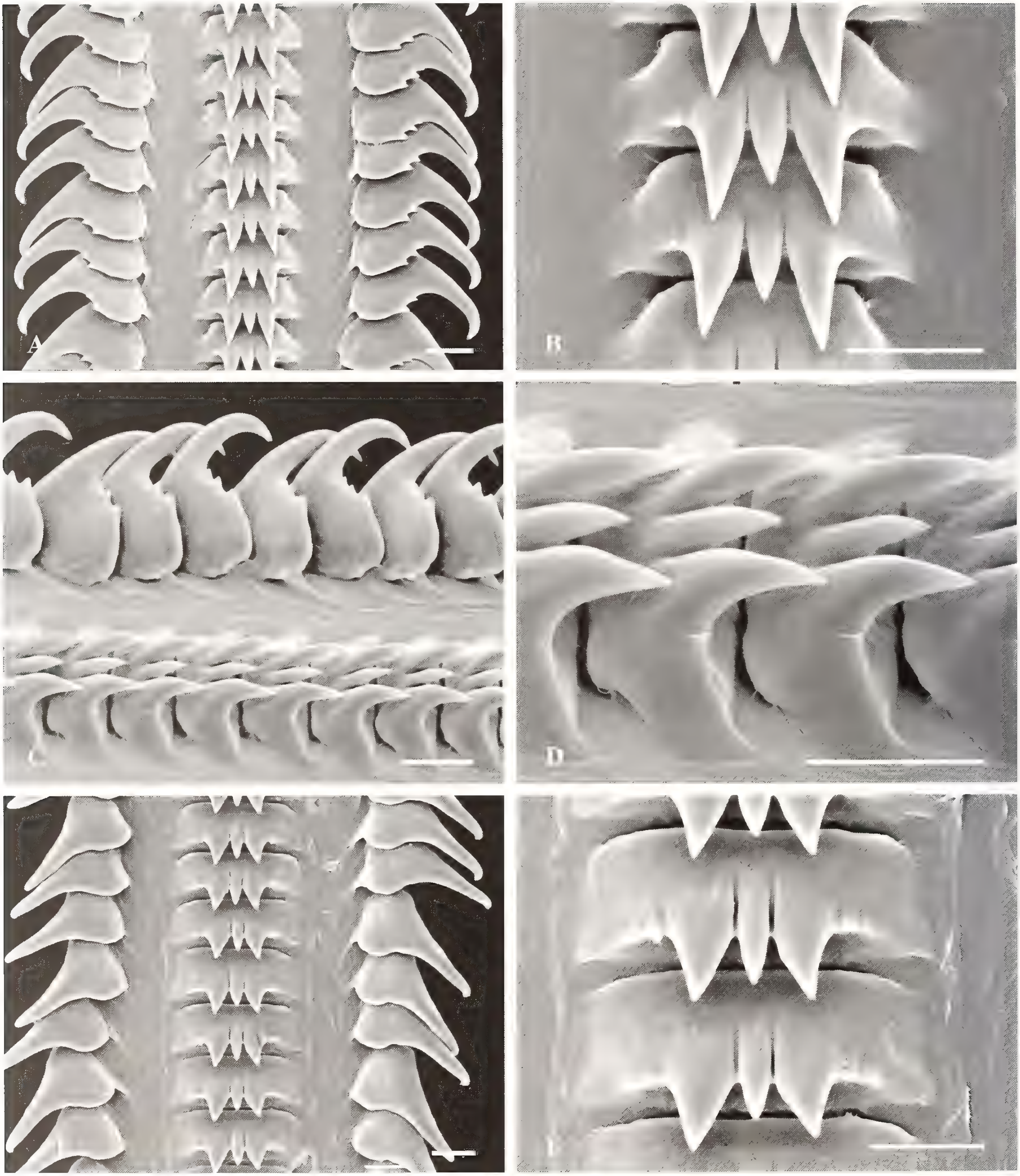


Figure 12. Scanning electron micrographs of the radulae of *Belloliva simplex* (A-D), New Caledonia, west coast, MONTROUZIER, st. 1318, 20-30 m (SL 4.1 mm), and *Belloliva iota* sp. nov. (E-F), Coral Sea, Lansdowne Bank, EBISCO, st. DW2631, 372-404 m (SL 7.2 mm). A, E, Dorsal view of the central part of the radular membrane. B, F, Enlarged rachidian teeth. C, D, Left lateral view of the rachidian teeth. Scale bars = 10 μm.

Distribution

Earlier known from the Tuamotu Islands, Tonga (Thiele 1929 in 1929-1931), and Western Samoa (Thiele 1929 in 1929-1931; 2 specimens from "Upolu" Samoa—Museum für Naturkunde, Humboldt University Berlin, ZMB 18.304; M. Glaubrecht pers. comm.), now recorded from the Loyalty Islands (Lifou) and northern and western New Caledonia, live in 10-45 m, shells down to 110-470 m.

Remarks

The original description is very brief and the accompanying illustration is uninformative. However, the identity of the species is established by the name-bearing type, and is confirmed by our examination of topotypical material from Anaa, Tuamotu Islands, in the collection of Jean Tröndle (La Force, France). Thiele's illustration (1929 in 1929-1931: fig. 384) of a specimen from western Samoa agrees with this material.

Belloliva simplex differs from its congeners by its very small adult size. It superficially resembles juveniles of *Belloliva exquisita*, with which it co-occurs at several stations, and from which it is readily distinguished by its smaller protoconch (1000 µm versus 1240-1580 µm in *B. exquisita*) and by its smooth, arcuate columella. For comparison with *Belloliva iota* sp. nov., see under that species.

Belloliva iota Kantor and Bouchet sp. nov.
(Figs. 12E-F, 13)

Type material

Holotype (Moll 9473) and 4 paratypes (Moll 9474) in MNHN.

Material examined

Coral Sea, Lansdowne Bank, MUSORSTOM 5, st. 388, 20°45′S, 160°54′E, 500-510 m (2 dd). EBISCO, st. DW2618, 20°06′S, 160°23′E, 280-304 m (2 dd; co-occurring with *Belloliva obeon* sp. nov.); st. DW2631, 21°03′S, 160°44′E, 372-404 m (4 lv); st. DW2639, 20°47′S, 161°01′E, 289-294 m (25 dd).

Type locality

Coral Sea, Lansdowne Bank, 20°47′S, 161°01′E, 289-294 m (EBISCO, st. DW2639).

Description (holotype)

Shell solid, glossy, elongate-oval (BWL/SL = 0.73, AL/SL = 0.59, D/SL = 0.46), with narrow aperture and elevated, somewhat turreted spire, consisting of approximately 0.5 protoconch and nearly 4 teleoconch whorls. Protoconch small, evenly rounded, diameter 820 µm, exposed height 580 µm, smooth, protoconch-teleoconch transition distinctly marked by onset of filament channel. Whorls moderately convex, evenly rounded, shoulder not pronounced. Filament channel completely open. Aperture lanceolate-oval, gradually narrowing adapically. Outer lip thickened, evenly convex in most of adapical part, nearly straight in median part and evenly rounded abapically. Parietal plate narrow, thin, anterior plating broadening in abapical part of aperture and having 4 plicae, adapicalmost being very weak. Color uniformly off-white.

Dimensions (holotype): SL 5.6 mm, SW 2.6 mm, BWL 4.1 mm, AL 3.3 mm. Largest specimen (MUSORSTOM 5, st. 388): SL 7.6 mm, SW 3.6 mm, BWL 5.5 mm, AL 4.6 mm.

One male specimen (EBISCO, st. DW2631, SL 7.2 mm, AL 4.4 mm; Fig. 13G) was dissected. General morphology similar to other studied congeners. Cephalic flaps with relatively large eyes. Penis long, exceeding the length of the mantle cavity, of even diameter along its length and obtuse at the tip. Gland of Leiblein narrow, tubular, slightly coiled anteriorly and nearly straight posteriorly, grey, opening into esophagus without constricted duct. Radula (Fig. 12E-F) about 85 µm wide (1.18% SL, 1.93% AL), consisting of 60 rows of teeth, of which 12-13 nascent; width of rachidian approximately 23 µm (27% of radular width). Rachidians narrowly spaced, cusps abutting the next tooth, anterior edge straight, lateral sides of basal plate gradually embedded in membrane without distinct border. Rachidian with short lateral flaps, 3 main cusps, central cusp narrower and 1.5 times shorter than lateral cusps, and a secondary, very small, indistinct cusp on each side of the main lateral cusps. Lateral teeth with broadened subtriangular bases and long, curved, hook-like cusps.

Distribution

Coral Sea, Lansdowne Bank, alive in 372-404 m, shells in 294-500 m.

Remarks

Belloliva iota varies only little in the degree of development of the plicae on anterior plating, which are nevertheless never very conspicuous. One of the specimens from the type locality has 3 extremely faint yellow axial zigzag lines. *Belloliva iota* sp. nov. differs from most congeners by its small adult size. It superficially resembles juveniles of *Belloliva exquisita*, from which it is readily distinguished by its smaller protoconch (800 µm versus 1240-1580 µm in *B. exquisita*). *Belloliva iota* sp. nov. differs from *Belloliva simplex* by its larger shell with slightly smaller protoconch, by the plicae on the anterior plating, and by its relatively smaller radula, consisting of smaller number of rows, with the rachidian teeth having nearly subrectangular lateral flaps (Fig. 12F) versus subtriangular ones in *B. simplex* (Fig. 12B), and in the absence of denticles at the bases of the cusps on the lateral teeth.

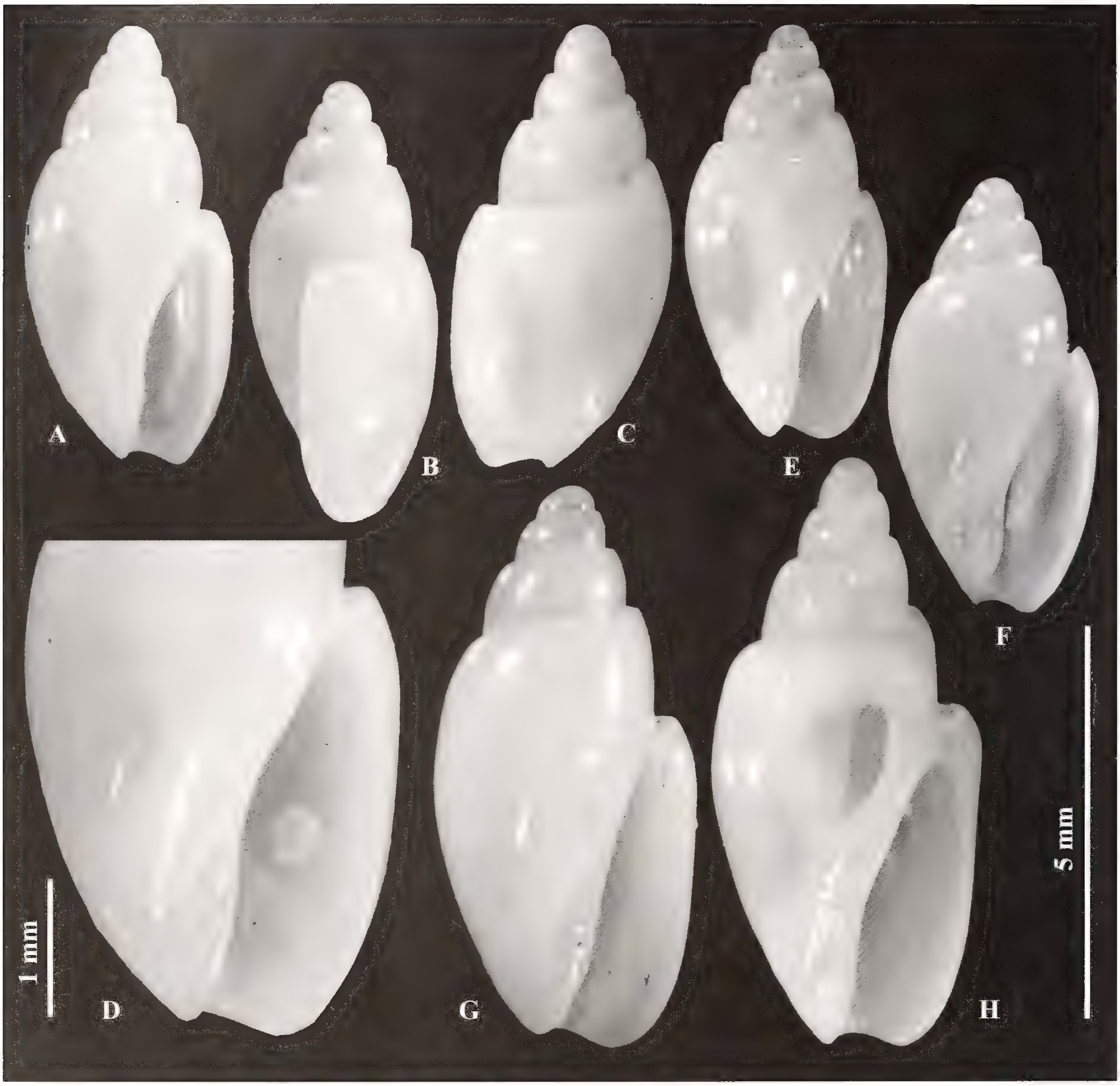


Figure 13. *Belloliva iota* sp. nov. A-D, Holotype. D, Detail of columellar region. E, Paratype, SL 5.4 mm. F, Paratype, SL 5.5 mm. G, EBISCO, st. DW2631, SL 7.1 mm. H, MUSORSTOM 5, st. 388, SL 7.6 mm. All shells illustrated at the same scale except D.

Etymology

From the Greek *iota*: very small; used as a noun in apposition.

Belloliva ellenae Kantor and Bouchet sp. nov.
(Figs. 14, 15, 16A-D)

Type material

Holotype (Moll 9475) in MNHN.

Material examined

Coral Sea, Chesterfield plateau: MUSORSTOM 5, st. 339, 19°53′S, 158°38′E, 380-395 m (2 dd); st. 361, 19°53′S, 158°38′E, 400 m (4 dd, 4 lv); st. 362, 19°53′S, 158°40′E, 410 m (5 dd); st. 379, 19°53′S, 158°40′E, 370-400 m (3 dd, 2 lv [holotype]). EBISCO, st. DW2596, 19°43′S, 158°37′E, 382-386 m (1 lv); st. DW2606, 19°36′S, 158°42′E, 442-443 m (3 lv, 3 dd); st. DW2607, 19°33′S, 158°40′E, 400-413 m

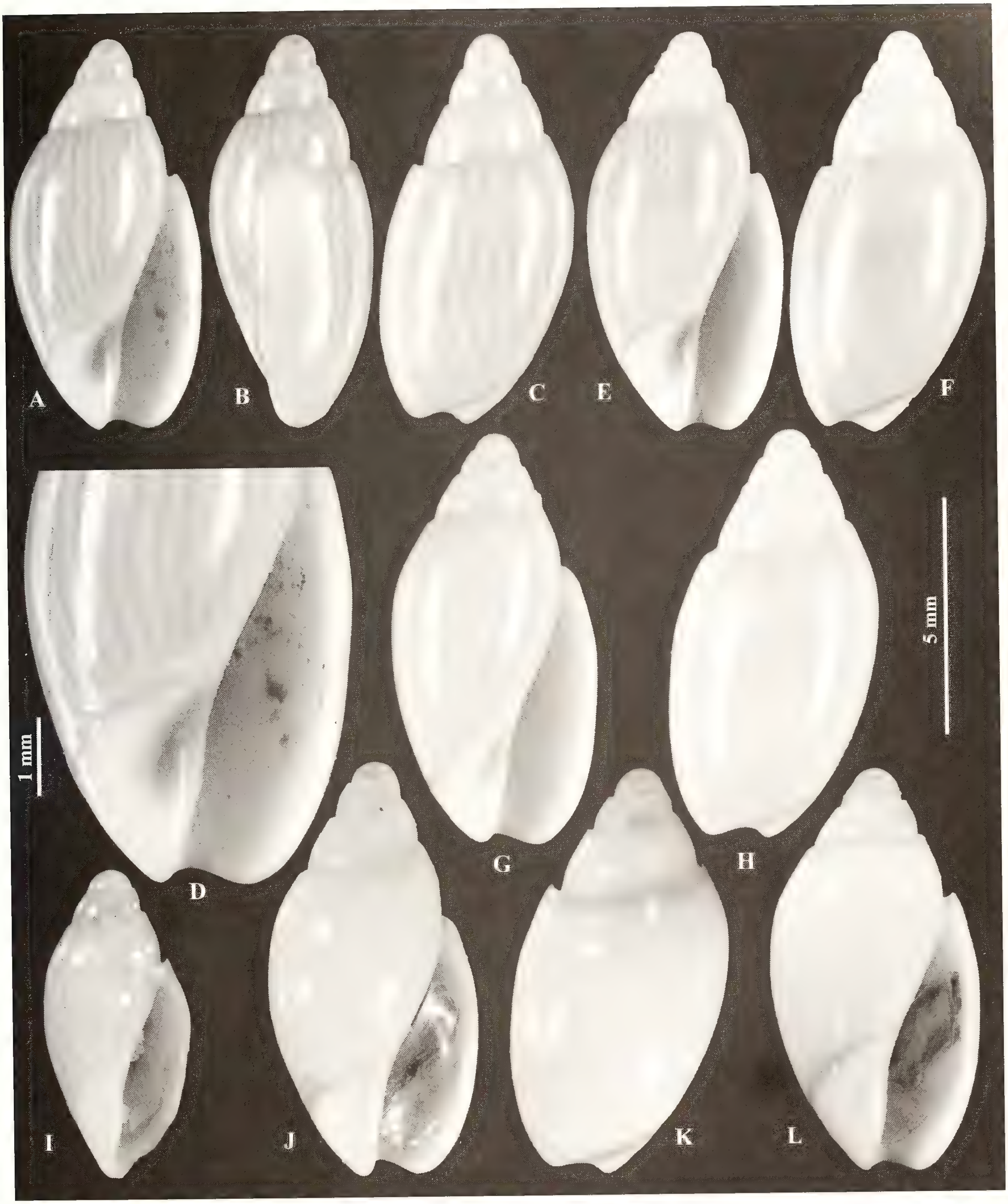


Figure 14. *Belloliva ellenae* sp. nov. A-D, Holotype. D, Detail of columellar region. E-H, MUSORSTOM 5, st. 361, SL 8.4 mm (E-F) and 8.6 mm (G-H). I, EBISCO, st. DW2596, intermediate between the "axially striped" and "pale" morphs, SL 6.5 mm. J-L, EBISCO, st. DW2610, "pale" morph, SL 8.8 mm (J) and 8.5 mm (K-L). All shells illustrated at the same scale except D.

(13 lv); st. DW2610, 19°34′S, 158°41′E, 486-494 m (39 lv, 13 dd).

Type locality

Coral Sea, Chesterfield plateau, 19°53′S, 158°40′E, 370-400 m (MUSORSTOM 5, st. 379).

Description (holotype)

Shell solid, glossy, oval-fusiform (BWL/SL = 0.80, AL/SL = 0.65, D/SL = 0.49), with moderately wide aperture and elevated spire, width 49% of height, consisting of about 1.0 protoconch and 4.0 teleoconch whorls. Protoconch rather large, evenly rounded, diameter 1170 μm, exposed height 920 μm, smooth, protoconch-teleoconch transition distinctly marked by onset of filament channel. Profile of whorls nearly straight, very slightly concave below suture, evenly rounded below inconspicuous shoulder. Filament channel completely open. Aperture lanceolate, gradually narrowing towards its tip. Outer lip nearly straight in most adapical 0.3, evenly rounded in lower part. Parietal plate narrow and thin, anterior plating broadening in lower part of aperture and having 7 poorly developed plicae. Background color light yellow. Last whorl and last half of penultimate whorl with distinct, closely spaced, slightly wavy darker yellow axial color lines (27 on last whorl). Near adapical margin of anterior band, lines distinctly opisthocline and their coaslescence forming a distinct color band. First half of penultimate whorl with gradually fading axial lines, early teleoconch whorls with only faint and irregularly spaced spots. Anterior plating with distinct elongated brown spot.

Dimensions (holotype): SL 8.2 mm, SW 4.0 mm, BWL 6.6 mm, AL 5.3 mm. Largest specimen (st. 361): SL 8.8 mm, SW 4.6 mm, BWL 7.2 mm, AL 6.2 mm.

Distribution

Coral Sea, Chesterfield plateau, alive in 386-486 m.

Remarks

Two distinct forms of *Belloliva ellenae* sp. nov. can be recognized. The "axially striped" form (Fig. 14A-H) has 26-46 colored axial lines on the last whorl and a dark spot on the anterior plating. The plicae on the anterior plating vary from nearly completely absent to moderately strong. The "pale" form is similar in shell outline to the typical form, but differs in color: the background is ivory and instead of axial lines there are two narrow light-brown color bands, one at the adapical limit of the anterior band, the other one on the rim of the filament channel; there is no columellar spot. Specimens of this form also differ by their somewhat larger protoconch and first teleoconch whorl (average D1 = 1.51 mm, range 1.45-1.56 mm in the "pale" form versus average D1 = 1.25 mm, range 1.17-1.29 mm in the "axially striped" form). The radulae (Fig. 16) and gross morphology are nearly identical in the two forms. The radula of a specimen of the "axially striped" form (MUSORSTOM 5, st. DW361,

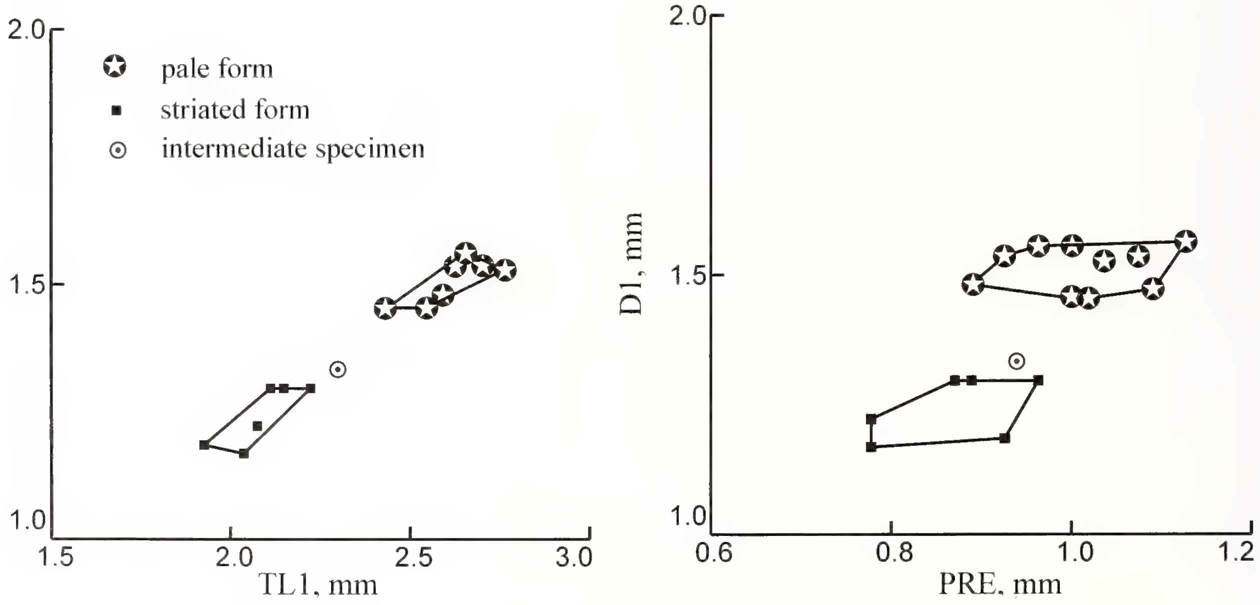


Figure 15. Comparison of "pale" and "axially striped" forms of *Belloliva ellenae* sp. nov. Ordinate: protoconch diameter (D1, mm); abscissa: (left) diameter of first teleoconch whorl (TL1) and (right) protoconch elevation (PRE).

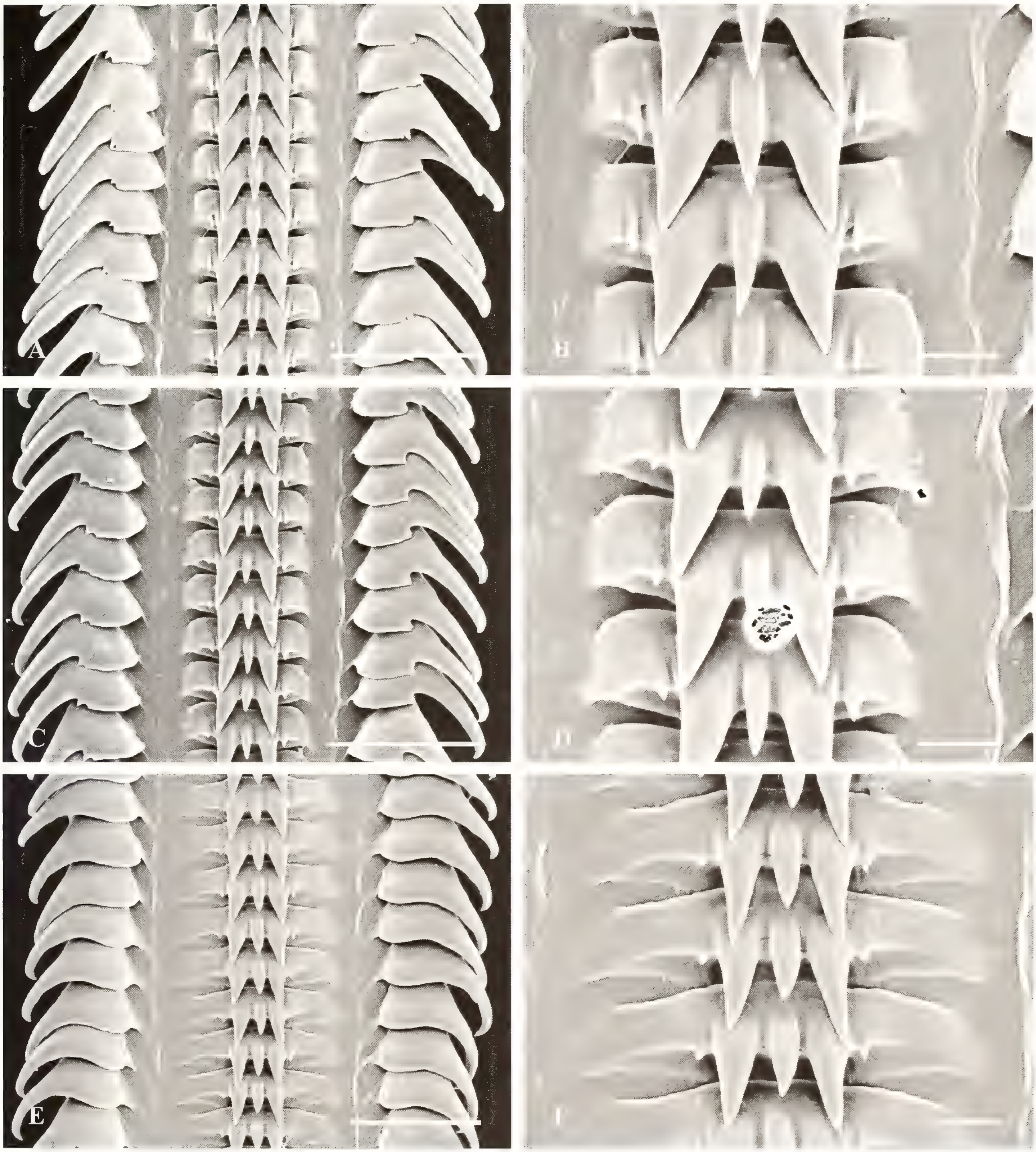


Figure 16. Scanning electron micrographs of the radulae of *Belloliva ellenae* sp. nov. (A-D) and *Belloliva dorcas* sp. nov. (E-F). A-B, "Axially striated" form (MUSORSTOM 5, st. DW361). C-D, "pale" form (EBISCO, st. DW2607). A, C, E, Dorsal view of the central part of the radular membrane, scale bars = 50 µm. B, D, F, Enlarged rachidian teeth, scale bars = 10 µm.

SL 8.6, AL 5.6 mm, male) was about 110 µm wide (1.27% of SL, 1.96% of AL) (Fig. 16A-B), consisting of 65 rows, of which 20 are nascent. Rachidians narrowly spaced, cusps abutting the previous tooth (Fig. 16B), anterior edge very slightly concave in its middle part and rounded at the edges. Lateral sides of basal plate gradually embedded into the membrane without distinct border. Rachidian with 3 broadly spaced main cusps, central cusp about 1.4 times shorter and much narrower than the lateral cusps, and one small, narrow, but distinct, additional cusp on each side of the main lateral cusps. Lateral teeth with subtriangular bases and long curved hook-like cusps bearing 1-2 small distinct denticles at their bases. The radula of the "pale" form (EBISCO, st. DW2607, SL 8.1, AL 5.4 mm, female) (Fig. 16C-D), was also about 110 µm broad (1.25% of SL, 1.96% of AL), consisting of 73 rows, of which 20 rows are nascent. Tooth shape was very similar to that of the "axially striped" form.

Both forms of *Belloliva ellenae* sp. nov. occur in a very limited area: the "axially striped" form was found at four stations that straddle only 3 km while the "pale" form was found at 3 stations spanning about 6 km, slightly to the north of the type locality. These two groups of stations are separated by 30 km. This distribution does not appear to be merely a sampling artifact, as hauls made during the EBISCO cruise at appropriate depths between the two areas were negative for *Belloliva ellenae* sp. nov., with the exception of a single specimen from a station (EBISCO, st. DW2596) situated right in the middle of the two clusters of stations. This specimen (Fig. 14I) is somewhat intermediate in coloration (axial lines are present but are very pale and the columellar spot is absent) and the dimensions of its protoconch and first teleoconch whorl are also intermediate (Fig. 15). This intermediate specimen from an intermediate locality is further evidence that the two forms are conspecific.

Belloliva ellenae sp. nov. is sympatric with *Belloliva obeon* sp. nov., *Belloliva dorcas* sp. nov., and *Belloliva exquisita*. It is readily distinguished from these, and from other congeners, by the combination of small adult size and color pattern (either of axial stripes and brown spot on anterior plating or of two narrow bands over ivory background).

Etymology

The species is named after our colleague Dr. Ellen E. Strong, curator at the National Museum of Natural History, Smithsonian Institution, Washington, D.C., and companion of the two authors during several field seasons.

Belloliva obeon Kantor and Bouchet sp. nov.

(Figs. 17, 18, 19, 20)

Type material

Holotype (Moll 9476) and 2 paratypes (Moll 9477) in MNHN.

Material examined

Coral Sea, Chesterfield Plateau, MUSORSTOM 5, st. 346, 19°40′S, 158°27′E, 245-252 m (3 dd [holotype and paratypes]); st. 388, 20°45′S, 160°54′E, 500-510 m (3 lv). EBISCO, st. DW2608, 19°33′S, 158°40′E, 393-396 m (5 dd, including 2 striped, co-occurring with *Belloliva dorcas* sp. nov.). Lansdowne Bank. CORAIL 2, st. DE16, 20°48′S, 160°56′E, 500 m (12 dd, 2 lv). EBISCO, st. DW2617, 20°06′S, 160°22′E, 427-505 m (8 dd, 1 lv striped); st. DW2618, 20°06′S, 160°23′E, 280-304 m (2 dd, striped; co-occurring with *Belloliva iota* sp. nov.); st. DW2619, 20°06′S, 160°23′E, 490-550 m (4 lv, striped); st. DW2625, 20°04.8′S, 160°20′E, 627-741 m (1 lv, striped); st. DW2629, 21°06′S, 160°46′E, 569-583 m (1 lv, 30 dd, striped).

Type locality

Coral Sea, Chesterfield Plateau, 19°40′S, 158°27′E, 245-252 m (MUSORSTOM 5, st. 346).

Description (holotype)

Shell medium-sized, solid, semitransparent in the central part of the last whorl, glossy, broadly oval (BWL/SL = 0.86, AL/SL = 0.70, D/SL = 0.52), with wide aperture and low spire, consisting of about 0.5 protoconch and 3.125 teleoconch whorls. Protoconch large, evenly rounded, diameter 1770 µm, exposed height 720 µm, smooth, protoconch-teleoconch transition distinctly marked by onset of filament channel. Profile of whorls very slightly concave subsuturally, with rather distinct rounded shoulder. Filament channel completely open. Aperture elongate-oval, gradually narrowing and rounded abapically. Outer lip slightly thickened, the edge itself sharp, slightly concave in most adapical part, nearly straight along most of its length and evenly rounded abapically. Parietal plait very narrow, hardly thickened, anterior plating clearly concave in profile, broadened, bearing ten pronounced plicae, diminishing in size adapically. Color uniformly off-white.

Dimensions (holotype largest specimen): SL 14.3 mm, SW 10.1 mm, BWL 12.4 mm, AL 10.1 mm.

Anatomy

The anatomy of two specimens (MUSORSTOM 5, st. 388, Chesterfield Plateau, SL 13.8, BWL, 12.2, AL 9.8, SW 7.3 mm; EBISCO, st. DW2619, Lansdowne Bank, SL 9.0, BWL 7.9, AL 6.3, SW 5.0 mm) was examined.

General morphology.—The body of the first one was badly torn during extraction, but the external morphology is similar to that of *Belloliva alaos* sp. nov. Foot thick, strongly contracted during fixation, propodium bent ventrally. Metapodium very broad, triangular-oval. Propodium crescent-

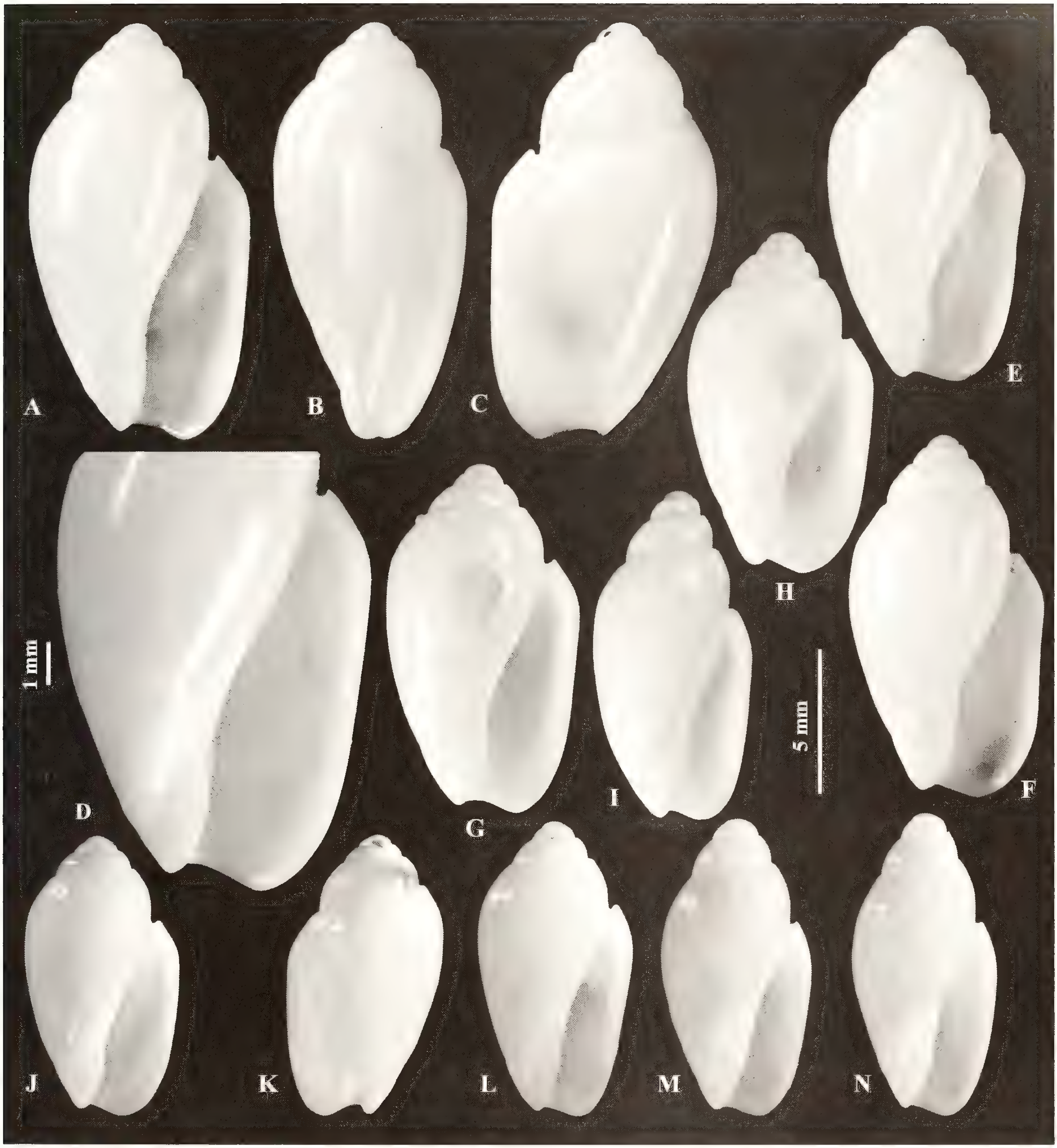


Figure 17. *Belloliva obeon* sp. nov. A-D, Holotype. E, Paratype, SL 12.3 mm. F, Paratype, SL 12.6 mm. G-I, CORAIL2, st. DE16, SL 12.0 mm (G), 11.8 mm (H), and 11.3 mm (I). J-N, EBISCO, st. DW2629: "typical," SL 9.6 mm (J-K), transitional, SL 10.1 mm (L), and slender specimens, SL 10.2 mm (M) and 10.4 mm (N). All shells illustrated at the same scale except D.

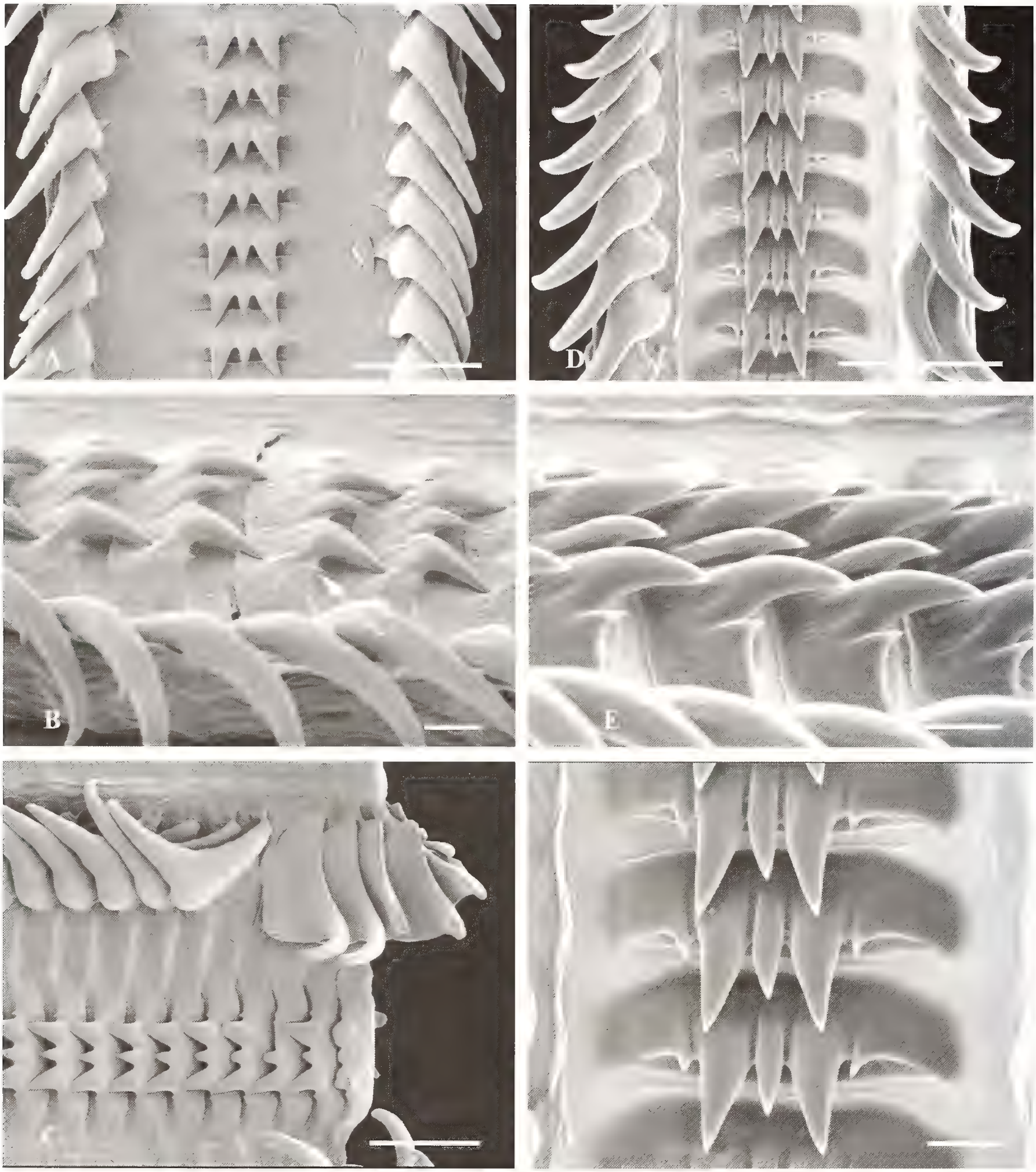


Figure 18. Scanning electron micrographs of the radula of *Belloliva obeon* sp. nov. [A-C, Coral Sea, Chesterfield Plateau, MUSORSTOM 5, 500-510 m, st. 388 (SL 13.8 mm); D-F, Coral Sea, Lansdowne Bank, EBISCO, st. DW2619 (SL 9.0)]. A, D, Dorsal views of the central portion of the radular ribbon. B, E, Left lateral view of the radular ribbon. C, Dorsal view of the bending plane of the radular ribbon. E, Dorsal view of enlarged central teeth. Arrow on B indicates additional cusp on the rachidian. Scale bars = 50 μm (A, C, D), 10 μm (B, E, F).

shaped, subdivided longitudinally by deep furrow and delimited from metapodium by dorsal and ventral grooves. Parapodia rather short in contracted state. Operculum very large, extremely thin and transparent, attached to opercular disc by narrow oval zone along its left side (about 0.5 of operculum width) (Fig. 19A). About 1/5 of posteriormost part of pad detached from dorsal surface of foot, forming a tongue-like extension. Head well set off from the foot (Fig. 19A), with broadly separated, laterally compressed flaps with large eyes. Columellar muscle thick, splitting into 3 branches in its posterior part.

Mantle cavity.—Mantle filament short. Anterior mantle tentacle and mantle lobe absent. Siphon long, narrow, and extending substantially beyond the evenly and slightly thickened mantle edge. Mantle itself very thin. Size and shape of osphradium and ctenidium very similar to those of *Belloliva alaos* sp. nov.

Alimentary system.—Organs of anterior foregut strongly contracted during fixation (Fig. 19B). Proboscis short with smooth walls. Salivary glands large, seemingly compact, fused around valve and posteriormost part of rhynchodeum, their structure ramified tubular, similar to that of *Belloliva*

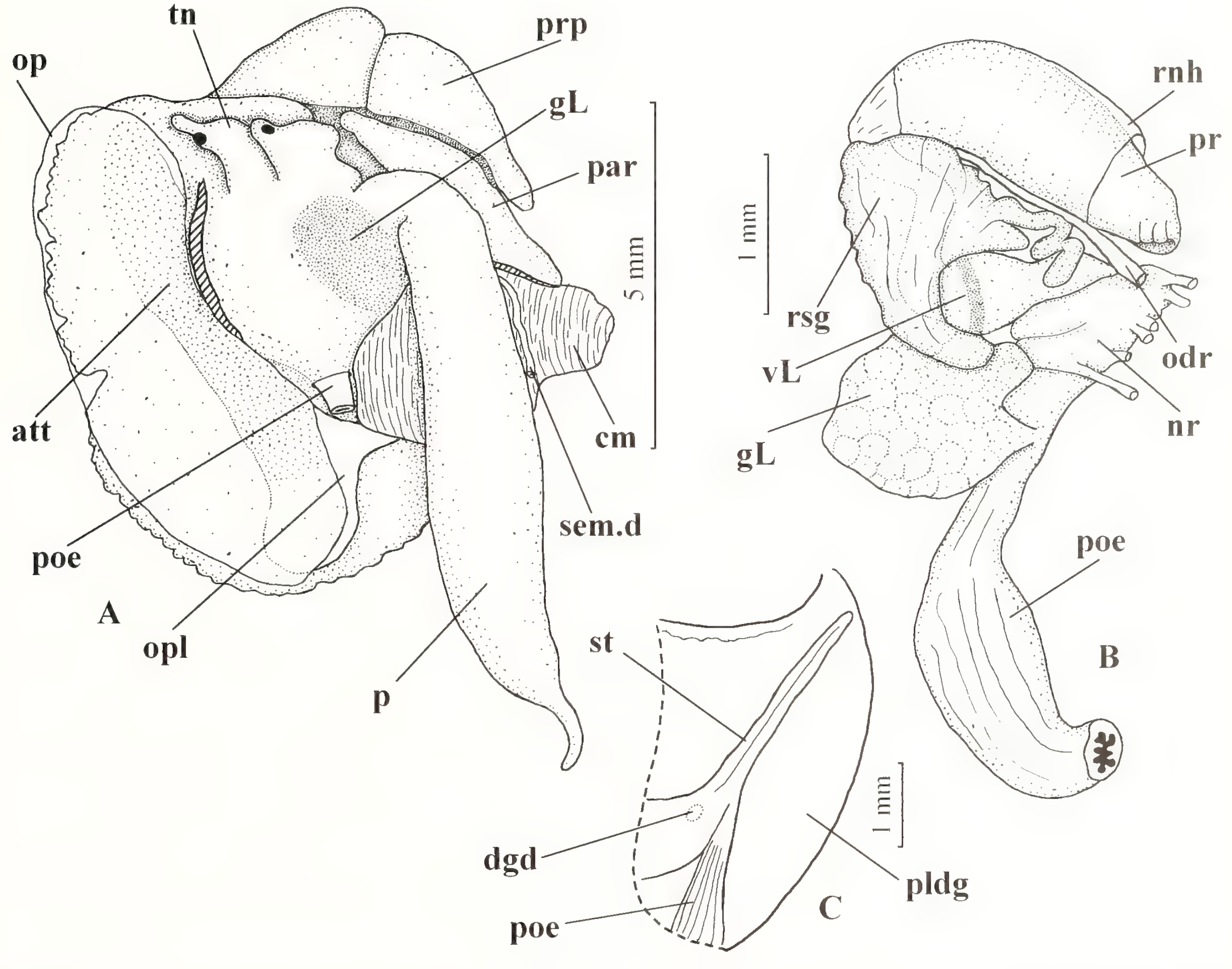


Figure 19. Some details of the morphology of *Belloliva obeon* sp. nov. A, Head-foot, dorsal view, mantle and visceral mass removed. B, Right view of the anterior foregut. C, External view of the stomach and part of the visceral mass. Abbreviations: att, attachment of the opercular pad to the operculum; cm, columellar muscle; dgd, opening of the digestive gland into stomach; gL, gland of Leiblein; nr, circumesophageal nerve ring; odr, odontophoral retractor; op, operculum; opl, opercular lobe; p, penis; par, parapodium; pldg, posterior lobe of digestive gland; poe, posterior esophagus; pr, proboscis; prp, propodium; rnh, rhynchodeum (= proboscis sheath); rsg, right salivary gland; sem.d, seminal duct; st, stomach; tn, cephalic tentacle; vL, valve of Leiblein.

brazieri. Accessory salivary glands absent. Gland of Leiblein large, massive, not coiled, dark brownish-grey, opening by narrow duct into esophagus. Large odontophoral retractor muscle passing ventrally under very thin-walled rhynchodeum. Valve of Leiblein large, pyriform. Odontophore large, about 2/3 of proboscis length, deeply withdrawn, as in *Amalda* (Kantor 1991). Radular diverticulum strongly cuticularized. Radula about 170 μm wide (1.23% of SL, 1.73% of AL), consisting of 52 rows of teeth. Rachidian about 70 μm wide (41% of radular width) with 3 main cusps, central cusp about 1.6 times shorter and narrower than the lateral cusps, and one very small, indistinct additional cusp on each side of the main lateral cusps, best seen in lateral view (Fig. 18B, indicated by arrow). Rachidians rather narrowly spaced, cusps strongly bent in profile, the tips of the lateral cusps resting on the following teeth (Fig. 18B). Anterior profile of the rachidian nearly straight in middle part and rounded at the edges, coinciding with anterior edge of basal plate. Lateral sides of basal plate gradually embedded into the membrane without distinct border. Lateral teeth with subtriangular bases and long curved hook-like cusps. Only part of stomach retrieved, characterized by very long and very narrow posterior mixing area (Fig. 19C).

Reproductive system.—Penis very long, flattened, simple, tapering towards the tip. Seminal papilla absent.

The specimen from Lansdowne is similar in outer morphology. The stomach is slightly larger, with an even longer posterior mixing area. Proboscis length about 2 mm. Radula slightly more than half of proboscis length, about 120 μm wide (1.33% of SL, 1.90% of AL), consisting of about 65 rows. Rachidian about 50 μm wide (42% of radular width) with 3 main cusps, central cusp about 1.6 times shorter and narrower than the lateral cusps, and one small, but distinct additional cusp on each side of the main lateral cusps. Rachidians rather narrowly spaced, cusps abutting the previous tooth, but tips not resting on it (Fig. 18E) as in the specimen from Chesterfield Plateau (Fig. 18B).

Distribution

Coral Sea, Chesterfield Plateau and Lansdowne Bank (Fig. 20), alive in 500-627 m, shells from 252 m.

Remarks

Belloliva obeon sp. nov. is rather variable in terms of shell shape and coloration. The specimens from Chesterfield Plateau are mostly pure off-white (with the exception of one specimen from EBISCO st. DW2608 that has broad, light yellow, nearly axial stripes on the last part of the last whorl) and their shell shape is overall similar to the type material. On Lansdowne Bank, the species is more variable, especially in terms of shell shape. Some specimens are extremely similar to those from the Chesterfields, but most have moderately to strongly developed axial color stripes, sometimes extending over the whole shell, while the background color may differ from off white to light yellow. Slender specimens (e.g., Fig. 17N) resemble smaller specimens of *Belloliva dorcas* sp. nov. but a large sample (31 specimens) from EBISCO st. DW2629 (Fig. 17J-N) contains all transitions to "typical" broad specimens. Radular morphology is also similar between specimens from Chesterfield Plateau and Lansdowne Bank, although slight differences can be observed, especially in the shape of the cusps of the rachidian teeth, which are much more strongly bent in the specimen from Chesterfield (Fig. 18B) than in the specimen from Lansdowne (Fig. 18E). Such differences are smaller than differences with other similar species, especially *Belloliva dorcas* sp. nov. (Fig. 16E-F), and we consider them intraspecific.

The species superficially resembles *Belloliva alaos* sp. nov. from New Caledonia, differing in the well pronounced plication on the columellar plait, and in the presence of eyes. It also differs from all other species of *Belloliva* in its straight or sometimes slightly concave outer lip. For comparison with *Belloliva dorcas* sp. nov., see under that species.

Etymology

From the Greek for "egg;" used as a noun in apposition.

Belloliva dorcas Kantor and Bouchet sp. nov.
(Figs. 16E-F, 20, 21, 22)

Type material

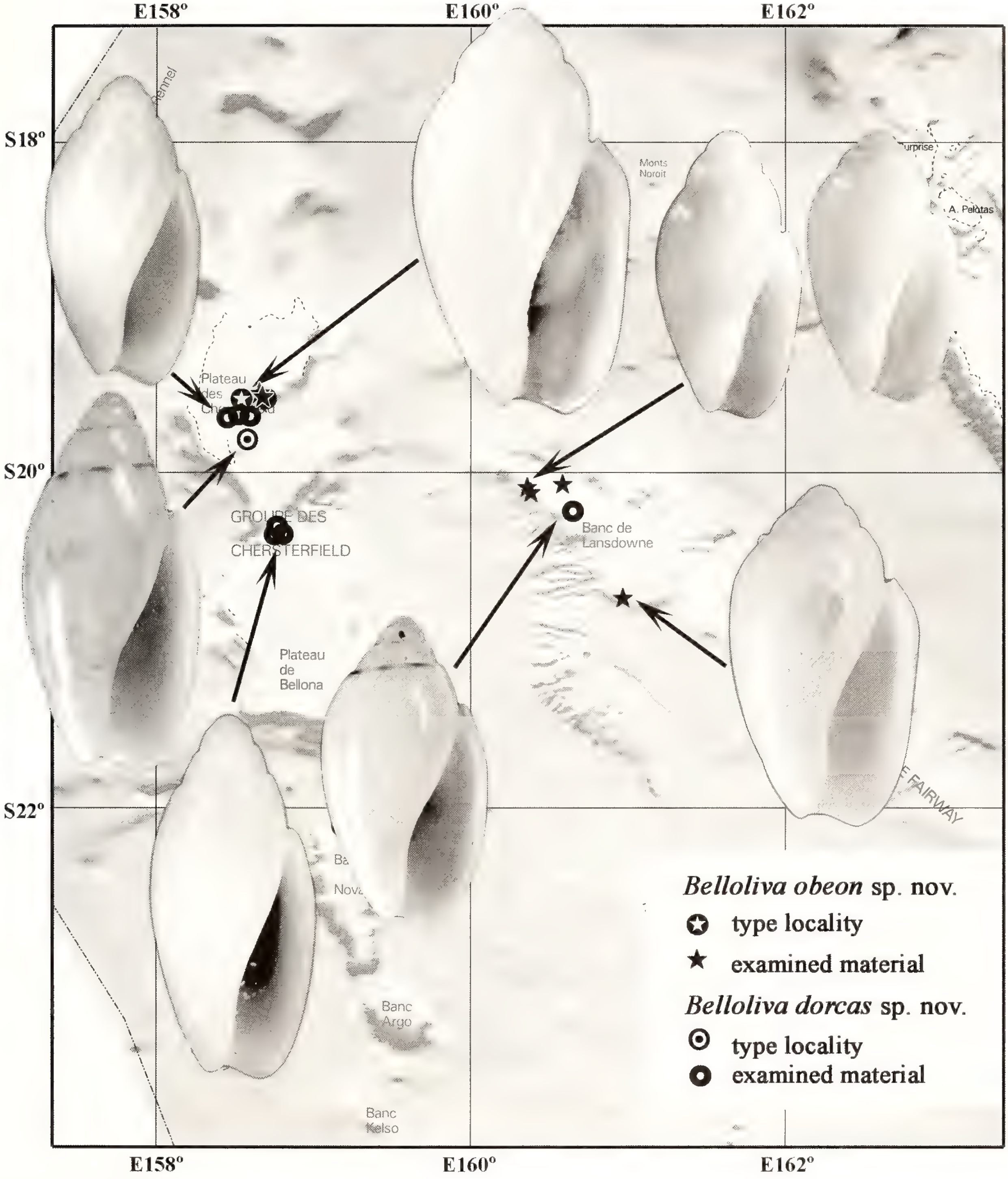
Holotype (Moll 9478) and 1 paratype (Moll 9479) in MNHN.

Material examined

Coral Sea. Bellona Plateau. MUSORSTOM 5, st. 328, 20°23′S, 158°44′E, 355-340 m (1 dd); st. 329, 20°23′S, 158°47′E, 320 m (1 dd); EBISCO, st. DW2564, 20°25′S, 158°41′E, 333-386 m (1 lv); st. DW2574, 20°20′S, 158°45′E, 358-374 m (1 lv, radula extracted, co-occurring with *Belloliva exquisita*). Chesterfield Plateau. MUSORSTOM 5, st. 347, 19°39′S, 158°28′E, 260 m (1 dd); st. 375, 19°52′S, 158°30′E, 300 m (3 dd [holotype and paratype]); CHALCAL 1984, st. D31, 19°33.5′S, 158°30.5′E, 230 m (1 dd.). EBISCO, st. DW2608, 19°33′S, 158°40′E, 393-396 m (1 dd, co-occurring with *Belloliva obeon* sp. nov.). Lansdowne Bank. MUSORSTOM 5, st. 389, 20°45′S, 160°54′E, 500 m (4 dd).

Type locality

Coral Sea, Chesterfield Plateau, 19°52′S, 158°30′E, 300 m (MUSORSTOM 5, st. 375).


E158°
E160°
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Rennel
Monts Noroit
A. Pelotas
Plateau des
GROUPE DES CHERSTERFIELD
Banc de Lansdowne
Plateau de Bellona
Banc Argo
Banc Kelso
FAIRWAY
Belloliva obeon sp. nov.
✪ type locality
★ examined material
Belloliva dorcas sp. nov.
⊙ type locality
● examined material
E158°
E160°
E162°

Figure 20. Distributions of *Belloliva obeon* sp. nov. and *Belloliva dorcas* sp. nov.

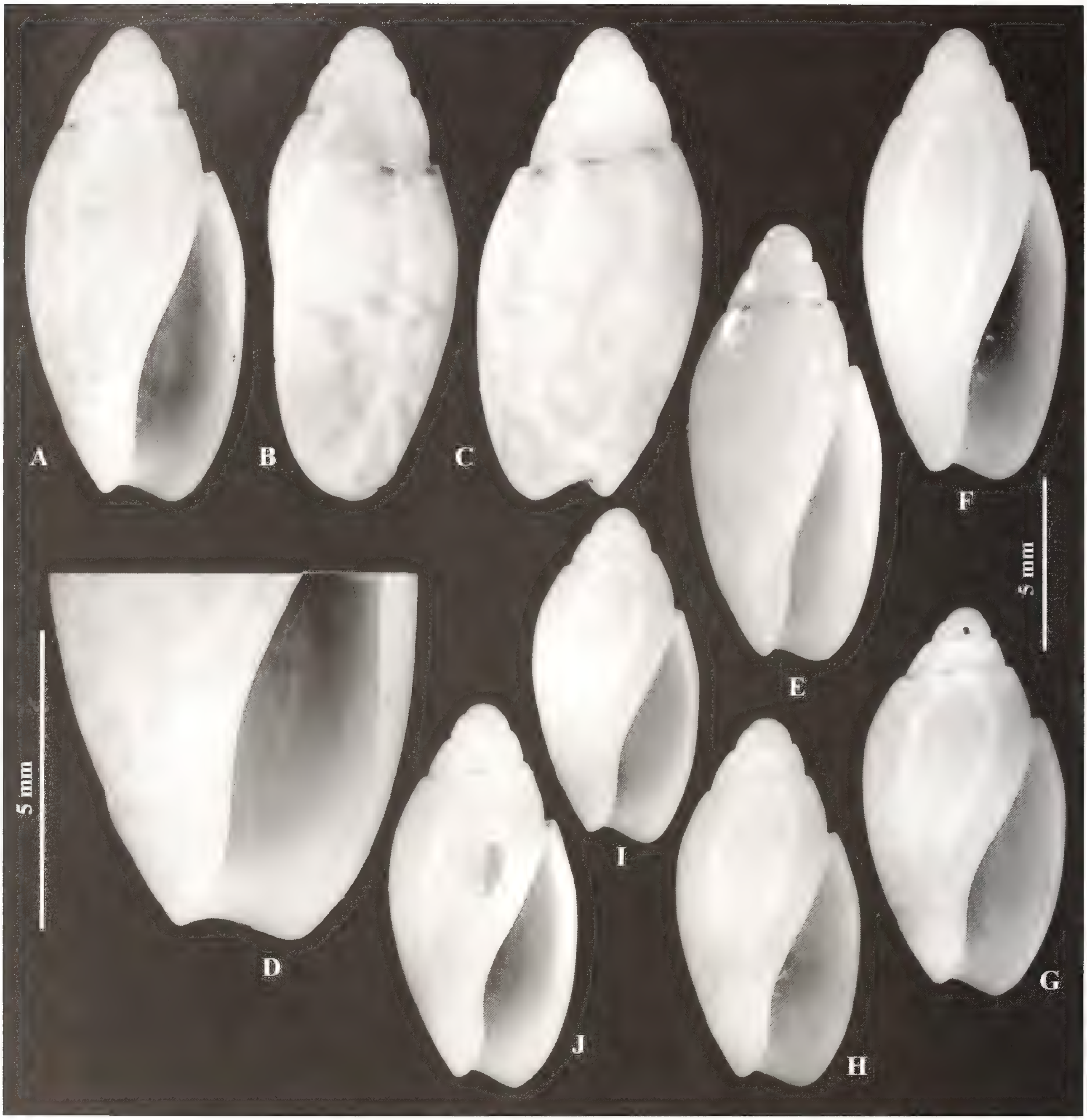


Figure 21. *Belloliva dorcas* sp. nov. A-D, Holotype, MUSORSTOM 5, sta. 375, SL 13.6 mm. E, Bellona Plateau, EBISCO sta. DW2574 (SL 12.5 mm, radula studied). F, Chesterfield Plateau, MUSORSTOM 5, sta. 328, SL 11.1 mm. G, H, Specimens from Lansdowne Bank (MUSORSTOM 5, sta. 389). G, (SL 11.1 mm). H, (SL 10.6 mm). I-J, Cheesterfield Plateau. I, CHALCAL, st. D31 (SL 9.6 mm). J, Chesterfield Plateau, MUSORSTOM 5, sta. 347 (SL 11.0 mm). All shells illustrated at the same scale except D.

Description (holotype)

Shell large, solid, glossy, elongate-oval (BWL/SL = 0.78, AL/SL = 0.69, D/SL = 0.45), with moderately narrow aperture and elevated spire, consisting of about 0.75 protoconch and 3 teleoconch whorls. Protoconch large, evenly rounded, diameter 1970 µm, exposed height 1070 µm, smooth, protoconch-teleoconch transition distinctly marked by onset of filament channel. Profile of whorls moderately convex, evenly rounded. Filament channel completely open. Aperture lanceolate-oval, gradually tapering adapically. Outer lip slightly convex, nearly straight in adapical-most part, evenly rounded abapically. Parietal plate very narrow, not visible in strictly ventral view, very thin, anterior plating thickening and broadening in abapical part of aperture, bearing 6 weak plicae (Fig. 21D). Background color creamy yellow. Last and penultimate whorls (except anterior plating) covered by distinct, rather broad, and irregularly shaped zigzag brown lines, well pronounced on the anterior band. Rim of filament channel marked by row of irregularly spaced brown spots or dashes.

Dimensions (holotype): SL 13.6 mm, SW 6.1 mm, BWL 10.6 mm, AL 9.4 mm. Largest specimen (paratype): SL 14.0 mm, SW 6.3 mm, BWL 11.1 mm, AL 9.6 mm.

Anatomy

Part of the body was retrieved from one specimen (EBISCO sta. 2574, SL 12.5 mm, AL 8.5 mm - shell see Fig. 21E). External morphology very similar to that of *Belloliva obeon*, including the presence of eyes. Penis differing from that of *B. obeon* in being of nearly even diameter along its length, obtuse at the tip, and lacking the attenuated tip. Gland of Leiblein long, tubular, slightly coiled, with strong transverse folds visible through the gland wall. Radula (Fig. 16E-F) about 140 µm wide (1.12% of SL, 1.64% of AL), consisting of about 85 rows of teeth, including 6 nascent. Rachidians rather narrowly spaced, cusps strongly abutting previous teeth (Fig. 16F). Anterior edge of rachidian slightly convex and rounded at the edges. Lateral sides of basal plate gradually embedded into the membrane without distinct border. Rachidian about 68 µm wide (49% of radula width) with 3 main, closely spaced cusps and broad lateral flaps, central cusp about 1.3 times shorter and narrower than lateral cusps, and one small, but distinct, additional cusp on each side of main lateral cusps. Lateral teeth with subtriangular bases and long, curved, hook-like cusps.

Distribution

Coral Sea, northern Bellona Plateau, Chesterfield Plateau, and Lansdowne Bank (Fig. 20), alive in 358-374 m, shells from 230 m.

Remarks

Belloliva dorcas sp. nov. is variable in terms of shell shape and coloration. The holotype has the most pronounced zigzag lines; in other specimens, these are either rather inconspicuous (Fig. 21G) or completely absent, the shell then being nearly white with only a row of small light brown dots at the rim of the filament channel (Fig. 21F).

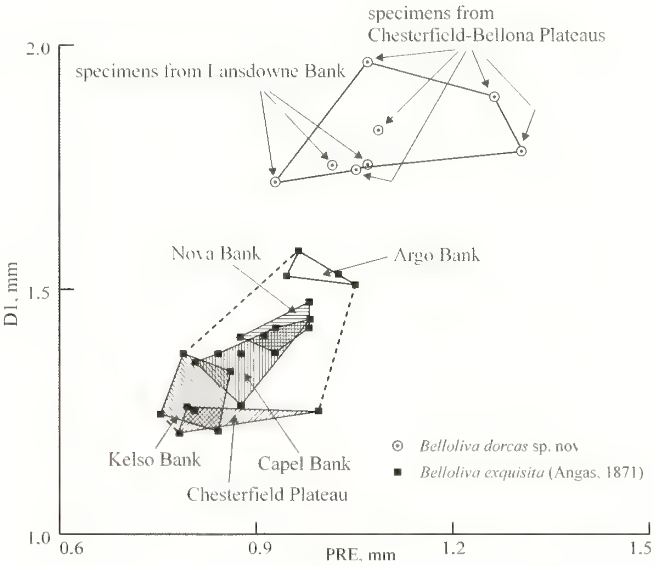


Figure 22. Morphometric comparison of protoconch dimensions of *Belloliva dorcas* sp. nov. and different populations of *Belloliva exquisita* (Angas, 1871) from the Coral Sea.

On the Chesterfield Plateau, *Belloliva dorcas* sp. nov. and *Belloliva obeon* sp. nov. are easily recognized on the basis of shell shape, shell color, and radular morphology. In *B. dorcas* sp. nov., the shape of the rachidian is rather distinct in having much broader lateral flaps compared to *B. obeon* sp. nov. and the other species studied here. The radular membrane is also somewhat narrower in *B. dorcas* sp. nov. (1.12% of SL and 1.64% of AL versus 1.23-1.33% of SL, and 1.73%-1.90% of AL in *B. obeon*). Their co-occurrence at one station (EBISCO, st. DW2608) is additional evidence that they are distinct species and not variants. On Lansdowne Bank, the identity of a population that we attribute to *Belloliva dorcas* sp. nov. (Fig. 21G-H) is problematic and requires anatomical or molecular confirmation. Sympatric, but not syntopic, specimens of *B. obeon* sp. nov. (Fig. 17M-N), superficially ressemble it by their broad, rather straight, axial stripes (rather than the narrow, zigzag, chevron lines of *B. dorcas*); the characteristic row of irregularly spaced brown spots or dashes on the rim of the filament channel are another reason why we attribute this lot to *B. dorcas*.

Belloliva exquisita bears a rather strong resemblance to *Belloliva dorcas*, of which it superficially seems to be a diminutive form. The two species differ in protoconch morphometrics, with a significant gap in their diameters (Fig. 22). The two species are sympatric on the northern Bellona and Chesterfield Plateaus, and even syntopic at one station (EBISCO st. DW2574), thus leaving no doubt that two different species are involved.

The COI sequence was obtained for *Belloliva dorcas* (voucher specimen MNHN Moll 9484—Fig. 21E), GenBank accession no. DQ780463.

Etymology

From the Greek noun *dorcas*, designating a kind of gazelle, with reference to the elegant colour pattern; used as a noun in apposition.

Belloliva exquisita (Angas, 1871)
(Figs. 22, 23, 24, 25, 26)

Olivella exquisuta Angas 1871: 13, pl. 1, fig. 2.

Type material

Holotype BMNH 1871.7.5.5 (Fig. 23A-C).

Material examined

Surprise Atoll: LAGON, st. 444, 18°15′S, 162°59′E, 300-350 m (1 dd); st. 502, 19°08′S, 163°30′E, 190 m (1 dd). PALEOSUPRISE, st. CP1391, 18°29.8′S, 163°02′E, 365 m (2 dd); st. CP1392, 18°29.8′S, 163°02.7′E, 370 m (1 dd).

North of New Caledonia: MUSORSTOM 4, st. DW142, 18°35′S, 163°10′E, 525 m (1 dd); st. DW149, 19°08′S, 163°23′E, 155 m (5 dd); st. DW150, 19°07′S, 163°22′E, 110 m (6 dd); st. DW151, 19°07′S, 163°22′E, 200 m (4 dd); st. DW162, 18°35′S, 163°10′E, 525 m (1 dd); st. DW164, 18°33′S, 163°13′E, 255 m (1 dd); st. DW184, 19°04′S, 163°27′E, 260 m (28 dd, 3 lv [1 specimen dissected]). BATHUS 4, st. DW923, 18°52′S, 163°24′E, 470-502 m (5 dd [co-occurring with *Belloliva simplex* and *Belloliva apoma*]); st. DW926, 18°57′S, 163°25′E, 325-330 m (1 dd); st. DW927, 18°56′S, 163°22′E, 444-452 m (1 dd); st. DW940, 19°00′S, 163°26′E, 305 m (4 dd, 1 lv); st. DW941, 19°02′S, 163°27′E, 270 m (1 dd); st. DW942, 19°04′S, 163°27′E, 264-270 m (11 dd).

New Caledonia proper: BATHUS 4, st. DW887, 21°07′S, 164°28′E, 320-344 m (2 dd [co-occurring with *Belloliva simplex*]). BATHUS 1, st. DW 688, 20°33′S, 165°00′E, 270-282 m (1 dd). West coast. EXPEDITION MONTROUZIER, st. 1304, 20°38.6′S, 164°13.2′E, 12-15 m (1 dd); st. 1311, 20°40.4′S, 164°14.9′E, 10-60 m (14 lv and dd) (co-occurring with *B. simplex*); st. 1312, 20°40.4′S, 164°14.9′E, 26-40 m (36 lv and dd) (co-occurring with *B. simplex*); st. 1319, 20°44.7′S, 164°15.5′E, 15-20 m (1 lv); st. 1321, 20°40.7′S, 164°14.9′E, 90-115 m (1 lv); st. 1322, 20°44.2′S, 164°15.2′E, 53-71 m (1 dd) (co-occurring with *B. simplex*); st. 1323, 20°40.9′S, 164°14.8′E, 82-120 m (4 dd); st. 1331, 20°40.0′-20°40.6′S, 164°11.2′-164°12.1′E, 55-57 m (4 lv) (co-occurring with *B. simplex*).

South of New Caledonia/Norfolk Ridge: MUSORSTOM 4, st. DW210, 22°44′S, 167°09′E, 340-345 m (1 dd, 1 lv). BIOCAL, st. DW41, 22°45′S, 167°12′E, 380-410 m (1 dd). BERYX 11, st. CH41, 23°39′S, 168°00′E, 230-360 m (1 dd). SMIB 5, st. DW79, 23°41′S, 168°01′E, 285 m (2 dd); st. DW80, 23°42′S, 168°00′E, 300 m (2 dd). East Jumeau Bank SMIB 8, st. DW170-172, 23°41′S, 168°00′-168°01′E, 230-290 m (4 dd); st. DW176, 23°42′S, 168°01′E, 283-290 m (1 dd); NORFOLK 1, st. DW1674, 23°40′S, 168°00′E, 245-253 m (1 dd). Antigonia Bank, NORFOLK 1, st. DW1712, 23°23′S, 168°02′E, 180-250 m (1 dd); st. DW1717, 23°23′S, 168°02′E, 250-312 m (1 dd). Banc P, NORFOLK 1, st. DW1723, 23°18′S, 168°15′E, 266-267 m (1 dd); st. DW1724, 23°17′S, 168°14′E, 200-291 m (1 dd); st. DW1726, 23°18′S, 168°15′E, 185-207 m (5 dd); st. DW1728, 23°19′S, 168°15′E, 207-276 m (4 dd).

Coral Sea, Capel Bank: MUSORSTOM 5, st. 256, 25°18′S, 159°53′E, 290-300 m (1 dd.); st. 258, 25°33′S, 159°46′E, 300 m (5 dd.), st. 263, 25°21′S, 159°46′E, 225-150 m (21 dd, 1 lv [radula and external morphology]); st. 265, 25°21′S, 159°45′E, 190-260 m (7 dd); st. 266, 25°20′S, 159°46′E, 240 m (3 dd, 2 lv); st. 270, 24°49′S, 159°34′E, 223 m (2 dd); st. 273, 24°43′S, 159°43′E, 290 m (3 dd); st. 274, 24°45′S, 159°41′E, 285 m (9 dd, 1 lv). Argo Bank: MUSORSTOM 5, st. 298, 22°44′S, 159°22′E, 320 m (2 dd); st. 299, 22°48′S, 159°24′E, 360-390 m (1 dd). Nova Bank: MUSORSTOM 5, st. 303, 22°12′S, 159°23′E, 332 m (1 dd). CHALCAL, st. D63, 22°11′S, 159°14′E, 305 m (4 dd). EBISCO, st. DW2522, 22°46′S, 159°21′E, 310-318 m (5 dd); st. DW2538, 22°20′S, 159°25′E, 318-323 m (5 dd). Kelso Bank: MUSORSTOM 5, st. 277, 24°11′S, 159°35′E, 270 m (10 dd, 1 lv); st. 280, 24°10′S, 159°36′E, 270 m (1 dd). EBISCO, st. DW2509, 24°08′S, 159°35′E, 265 m (1 dd); st. DW2514, 24°06′S, 159°41′E, 295-310 m (1 dd); st. DW2515, 24°04′S, 159°41′E, 330-370 m (1 dd). Bellona Plateau: EBISCO, st. DW 2547, 21°06′S, 158°36′E, 356-438 m (1 dd); st. DW2574, 20°20′S, 158°45′E, 358-374 m (1 dd, co-occurring with *Belloliva dorcas* sp. nov.); Chesterfield Plateau: EBISCO, st. DW 2603, 19°36′S, 158°43′E, 570-568 m (8 dd).

Type locality

Coogee Bay, New South Wales, Australia.

Description

Shell solid, relatively thin, glossy, with moderately narrow aperture and elevated spire. Protoconch large, evenly rounded, diameter 1200-1600 μm, smooth. Profile of whorls moderately convex, evenly rounded, very inconspicuously shouldered. Filament channel open. Aperture lanceolate-oval, gradually tapering adapically. Outer lip slightly convex, nearly straight in most adapical part, evenly rounded abapically. Anterior plating bearing 5-7 rather weak, but distinct plicae.

Dimensions: largest specimen (Capel Bank, MUSORSTOM 5, st. 258) SL 12.5 mm, SW 5.2 mm, BWL 10.2 mm, AL 8.1 mm.

Distribution

Southeastern Australia, New South Wales, Queensland; Coral Sea guyots, New Caledonia including its continuation

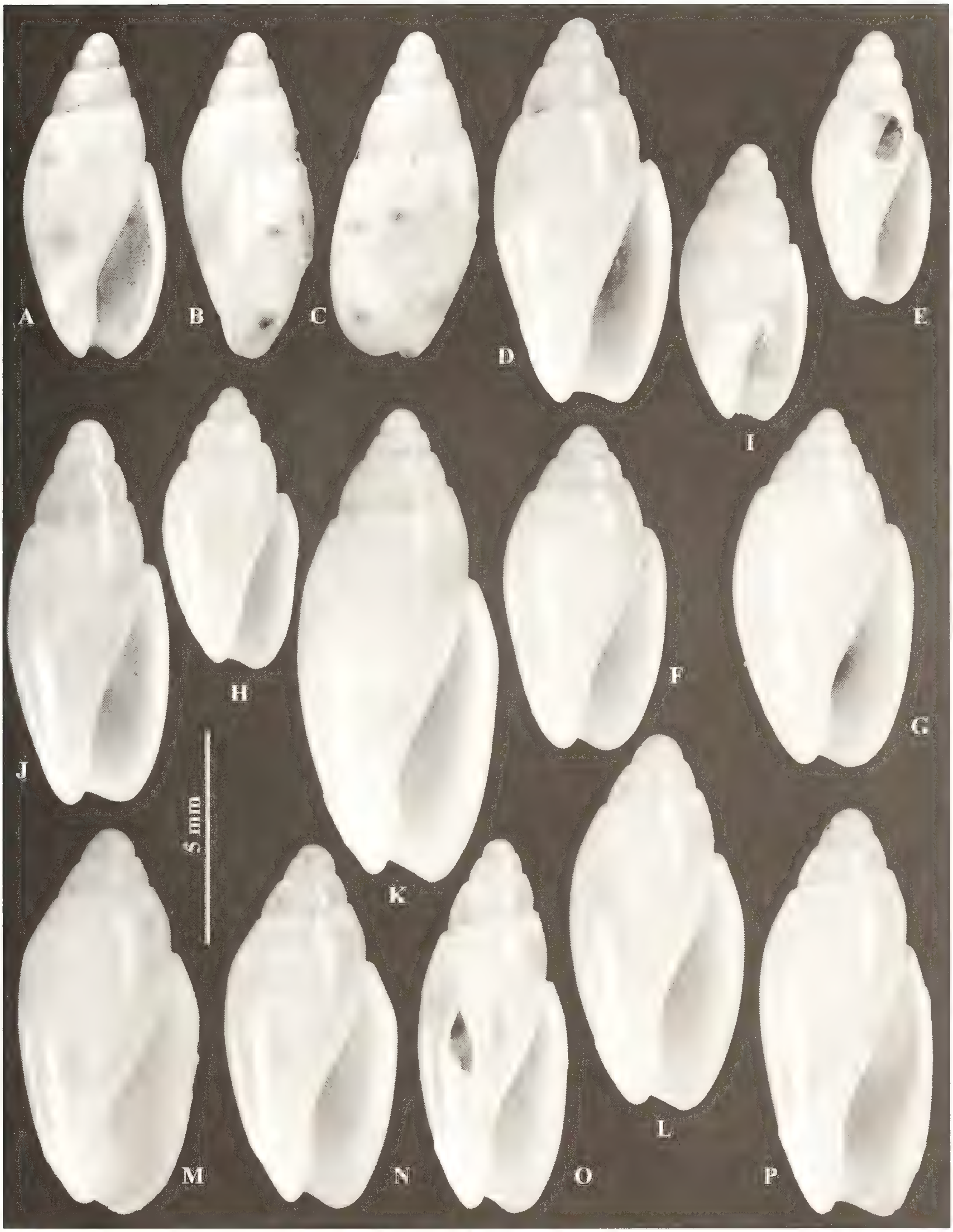


Figure 23. *Belloliva exquisita* (Angas, 1871). A-C, Holotype, BMNH 1871.7.5.5 (SL 7.7 mm). D, Northern New Caledonia, MUSORSTOM 4, st. DW184 (SL 9.2 mm). E, Northern New Caledonia, MUSORSTOM 4, st. DW149, SL 6.4 mm. F, G, Northern New Caledonia, MUSORSTOM 4, st. DW149, SL 7.6 and 8.4 mm. H, Northern New Caledonia, PALEO-SURPRISE, st. DW1391, SL 6.7 mm. I, Koumac, western New Caledonia, st. 1311 (SL 6.5 mm). J, Southern New Caledonia, SMIB5, st. DW80 (SL 9.2 mm). K, Capel Bank, MUSORSTOM 5, st. 258 (SL 11.2 mm). L, Capel Bank, MUSORSTOM 5, st. 265, SL 8.9 mm. M, Kelso Bank, MUSORSTOM 5, st. 277 (SL 9.0 mm). N, Kelso Bank, MUSORSTOM 5, st. 277 (SL 8.7 mm). O, Bank Nova, CHALCAL, st. D63 (SL 8.8 mm). P, Argo Bank, MUSORSTOM 5, st. 299 (SL 9.8 mm). All shells illustrated at the same scale.

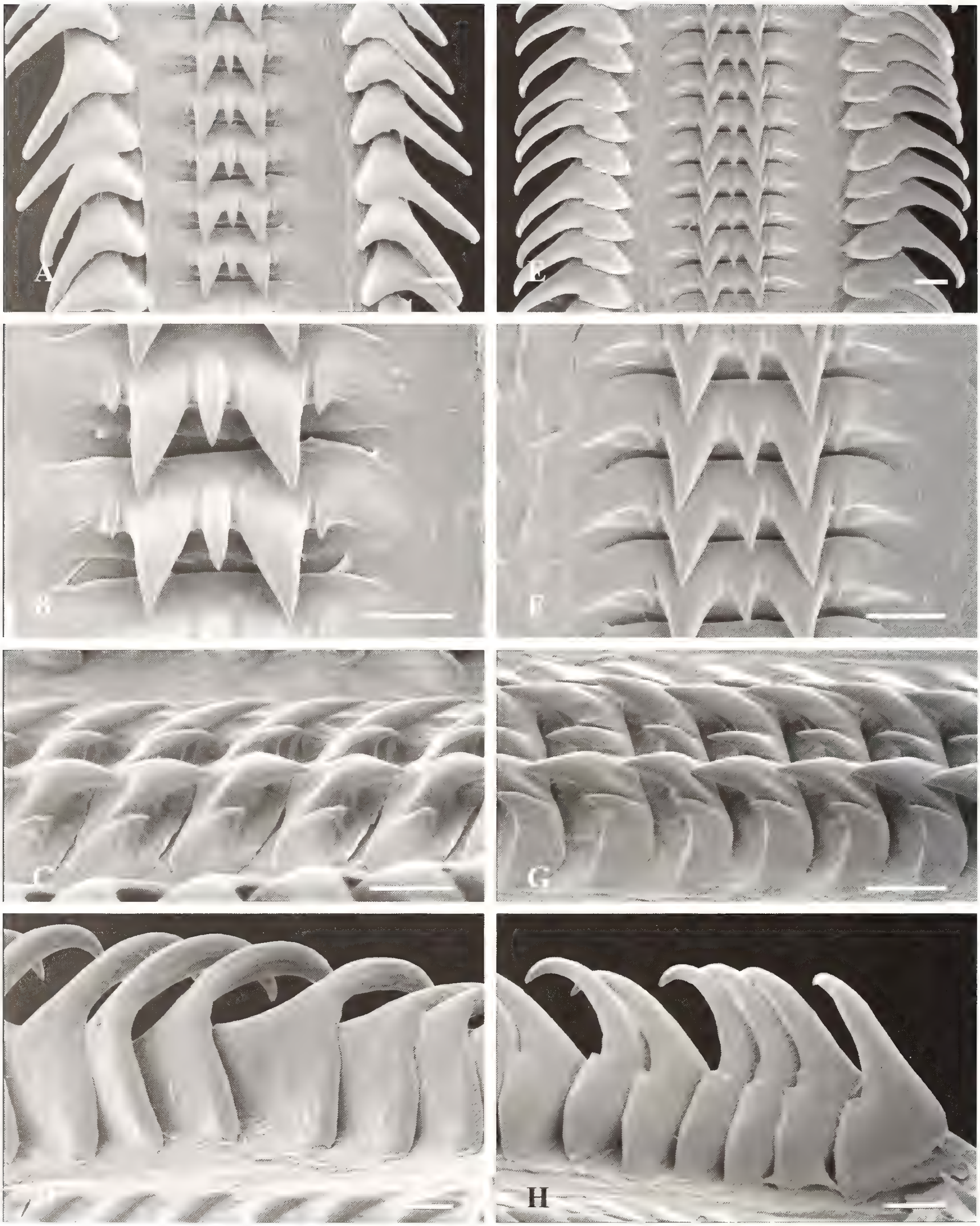


Figure 24. Scanning electron micrographs of the radula of *Belloliva exquisita* (Angas, 1871). A-D, Coral Sea, MUSORSTOM 5, sta. 263. E-H, Northern New Caledonia, MUSORSTOM 4, sta. DW 184. A, E, Dorsal view of the central part of the radular membrane. B, F, Enlarged rachidian teeth. C, G, Left and right lateral views of the rachidian teeth, respectively. D, H, Left and right lateral views of the lateral teeth, respectively. Scale bars = 10 μm.

to Surprise Atoll in the North and Norfolk Ridge in the South, alive 26-345 m, shells in 12-525 m.

Remarks

We are treating *Belloliva exquisita* as a single, highly variable species, both in terms of geographical and bathymetric variation. Within-population variation concerns coloration, with very pale to practically white or semitransparent specimens not uncommon in all parts of the distribution.

Most populations from off the north, south and west coasts of New Caledonia, including Norfolk Ridge, are very similar and there is no doubt that they represent a single species. Conchologically specimens from these populations are most similar to those from New South Wales, including the holotype (Fig. 23A-C). These individuals are characterized by rather slender shells (D/SL 0.45, n = 6, range 0.43-0.46) with elevated spires (BWL/SL 0.77, n = 6, range 0.75-0.78), and a color pattern typically of narrow, irregular zigzag brown lines on a creamy yellow background, and two spiral rows of unevenly spaced, spirally elongated, brown spots, one on rim of filament channel, the other on whorl periphery. Coloration is more pronounced in southern populations (Fig. 23J), although pale to nearly white specimens are also found there, but in lesser proportion than in the northern populations (Fig. 23H).

A little more problematic is a series of populations from a rather narrow depth range (110-190 m) in a restricted area extending for about 13 km (MUSORSTOM 4, st. DW 149, 150, 151) that differ from the "typical" form in having a larger, much broader shell (average D/SL = 0.50, n = 6, range 0.49-0.51, Fig. 23F, G; versus D/SL = 0.45, n = 6, range 0.43-0.46 in "typical" form) and sharper and more numerous plicae on the anterior plating. At one station (MUSORSTOM 4, st. DW 149) the broad and narrow (Fig. 23E) forms co-occur, which might indicate that they represent two different species. However, as only four empty shells were taken at that station, the evidence to treat them as two species is very weak and, in the absence of further data (radular morphology, anatomy), we prefer to hypothesize that the broad form represents a local variant of *Belloliva exquisita*. Ideally, this should be tested with molecular data.

Variation in the Coral Sea is more classically geographical, with each of the guyots having its own recognizable population, described below from south to north. However, the morphometries of specimens from different banks overlap and form a continuum with the "typical" form from New Caledonia (Fig. 25); we believe that this geographical variation reflects limited genetic exchange between banks, but not isolation.

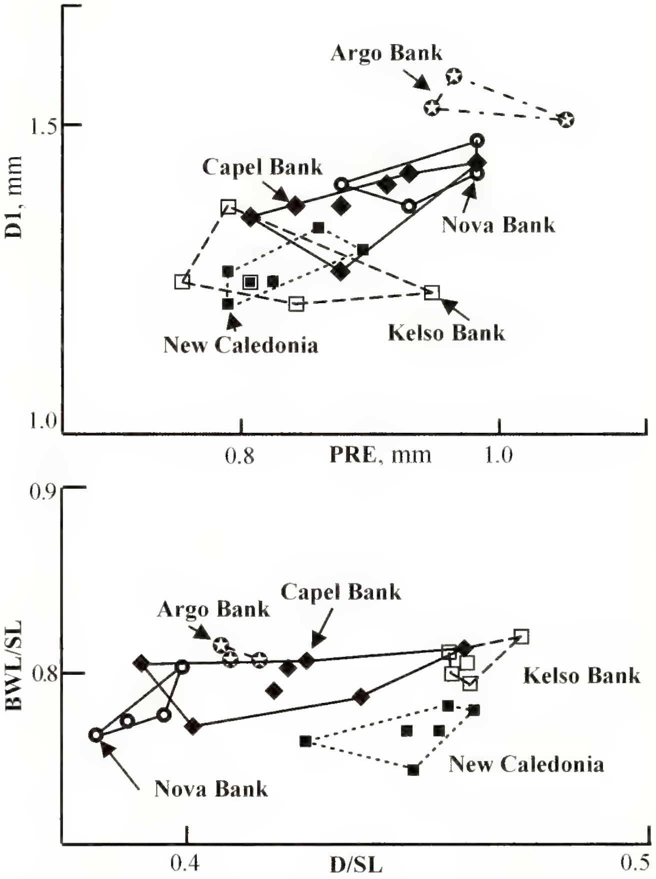


Figure 25. Morphometric comparisons of some protoconch and shell measurements of different populations of *Belloliva exquisita* (Angas, 1871) to illustrate the overlap of characters. Different populations are marked by different symbols.

Capel Bank (Fig. 23K, L). Shell to 12.5 mm in length, rather slender (D/SL 0.42, n = 7, range 0.39-0.46), with lower spire (BWL/SL 0.80, n = 7, range 0.77-0.81), usually pale, zigzag lines from very pale to absent, brown spots at channel rim present at least on parts of shell. Protoconch on average slightly larger (D1 = 1.37, n = 7, range 1.26-1.42) than in a "typical" form (D1 = 1.24, n = 6, range 1.21÷1.30), although both forms overlap significantly (Fig. 25).

Kelso Bank (Fig. 23M, N). Shells to 9.0 mm in length, differing from previous in their broader, more oval shell (D/SL in average 0.46, n = 5, range 0.46-0.47) with shorter spire, generally light in background color, although with better pronounced brown zigzag lines. Protoconch dimensions slightly smaller than in specimens from Capel Bank, but overlapping with "typical" form.

Argo Bank (Fig. 23N). Shells more similar in shape to those from Capel Bank, but characterized by the largest protoconch dimensions. Coloration light, zigzag lines pale, but well defined.

Nova Bank (Fig. 23O). Shells to 11.6 mm, characterized by rather slender shells (D/SL in average 0.39, n = 4, range 0.38-0.40). Protoconch dimensions completely overlaping with those from Capel Bank. Coloration light, some specimens with very pale zigzag lines.

Our material from Bellona and Chesterfield Plateaus is in rather poor condition and does not allow a detailed description, but is sufficient to record *Belloliva exquisita* in sympatry with *Belloliva dorcas* and to highlight the fact that the protoconch of these specimens is the smallest in all populations of *B. exquisita* examined (Fig. 22).

The anatomy of three specimens was examined, one from Capel Bank (MUSORSTOM 5, st. 263, SL 9.8, BWL 8.1, AL 6.2, SW 4.1), one from North of New Caledonia (MUSORSTOM 4, st. DW184, SL 9.4, BWL 7.2, AL 6.2, SW 4.2 mm), and one dried, rehydrated, specimen from Koumac (MONTROUZIER, st. 1312, SL 6.2, BWL 4.8, AL 4.3, SW 3.1 mm).

The specimen from the Coral Sea had the body strongly contracted, mantle cavity spanning about 0.5 whorls, nephridium 0.3 whorls, digestive gland with gonad about 3 whorls. Body in alcohol uniformly pale yellow, lacking pigmentation. Nephridium with transparent walls. Anterior lobe of digestive gland small, spanning about 0.3 whorls and completely separated from posterior lobe by stomach which is oriented obliquely with regard to columellar axis. Foot thick, strongly contracted during fixation, transversely folded, metapodium broadly triangular-oval, propodium small in comparison with metapodium, typically crescent-shaped, subdivided longitudinally. Operculum transparent, very thin, elongate, constricted abapically, slightly thickened along low inner edge. Head well distinguished from the rest of the body, with two large vertical flaps, bearing large eyes.

Mantle cavity.—Mantle strongly contracted, edge straight and thickened. Mantle thin, osphradium and ctenidium showing through it. Siphon very thin-walled, slightly extending beyond mantle edge, with smooth edges. General arrangement and proportions of organs in the mantle complex similar to that of *Belloliva alaos*.

Alimentary system.—Anterior foregut very similar to that of *Belloliva alaos*. Salivary glands apparently ramified-tubular. Accessory salivary glands absent. Radula consisting of about 75 rows of teeth, membrane width about 90 μm (0.92% SL, 1.45% AL). Rachidian with 3 main cusps, central cusp about twice as narrow and 1.5 times shorter than lateral cusps; an additional small but distinct cusp on each side of the main lateral cusps. Dorsal grooves on the main lateral cusps shallow and broad, best seen in lateral view (Figs. 24C, G). Anterior profile of rachidian nearly straight. Posterior edge of basal plate slightly convex. Sides of basal plate gradually embedded in the membrane without distinct border. Lateral teeth subtriangular with curved hook-like tips (Figs. 24D, H). Stomach large, spanning more than 0.5 whorl, with very long posterior mixing area. Stomach anatomy not examined in detail due to poor fixation. Rectal gland not found during dissection, probably obscured by thick mucous layer produced by hypobranchial gland.

Reproductive system.—Specimen a mature male, penis long, smooth, narrowing sharply towards its tip, similar to *Belloliva alaos*.

The external morphology of the two specimens from New Caledonia is very similar. Stomach similar in shape but much shorter. Digestive gland small, anterior spanning about 1/6 whorl, posterior about ¼ whorl. Upper 3 whorls occupied by testis. Seminal vesicle situated at lower corner of junction of digestive gland and testis, making several loops. Penis as long as mantle cavity, smooth, oval in section, ending in a small, nearly transparent, seminal papilla. Radula of both specimens identical and very similar to that of the Coral Sea specimen (Fig. 24E-H), differing only in the relatively broader, more triangular central cusp of the rachidian, as well as slightly wider radular membrane (membrane width 100 versus 95 μm, i.e., 1.06% versus 1.53% of SL and 1.61% versus 2.20% of AL).

Calyptoliva Kantor and Bouchet gen. nov.

Diagnosis

Shell small, 7-15 mm, narrowly elongate-oval, with attenuated spire. Suture narrowly channeled, overlaid by thin primary callus. Protoconch paucispiral, consisting of about one whorl, smooth, evenly rounded, large, diameter 1300-1650 μm, protoconch-teleoconch transition not clear. Aperture narrow, elongate. Parietal plate narrow, anterior plating smooth.

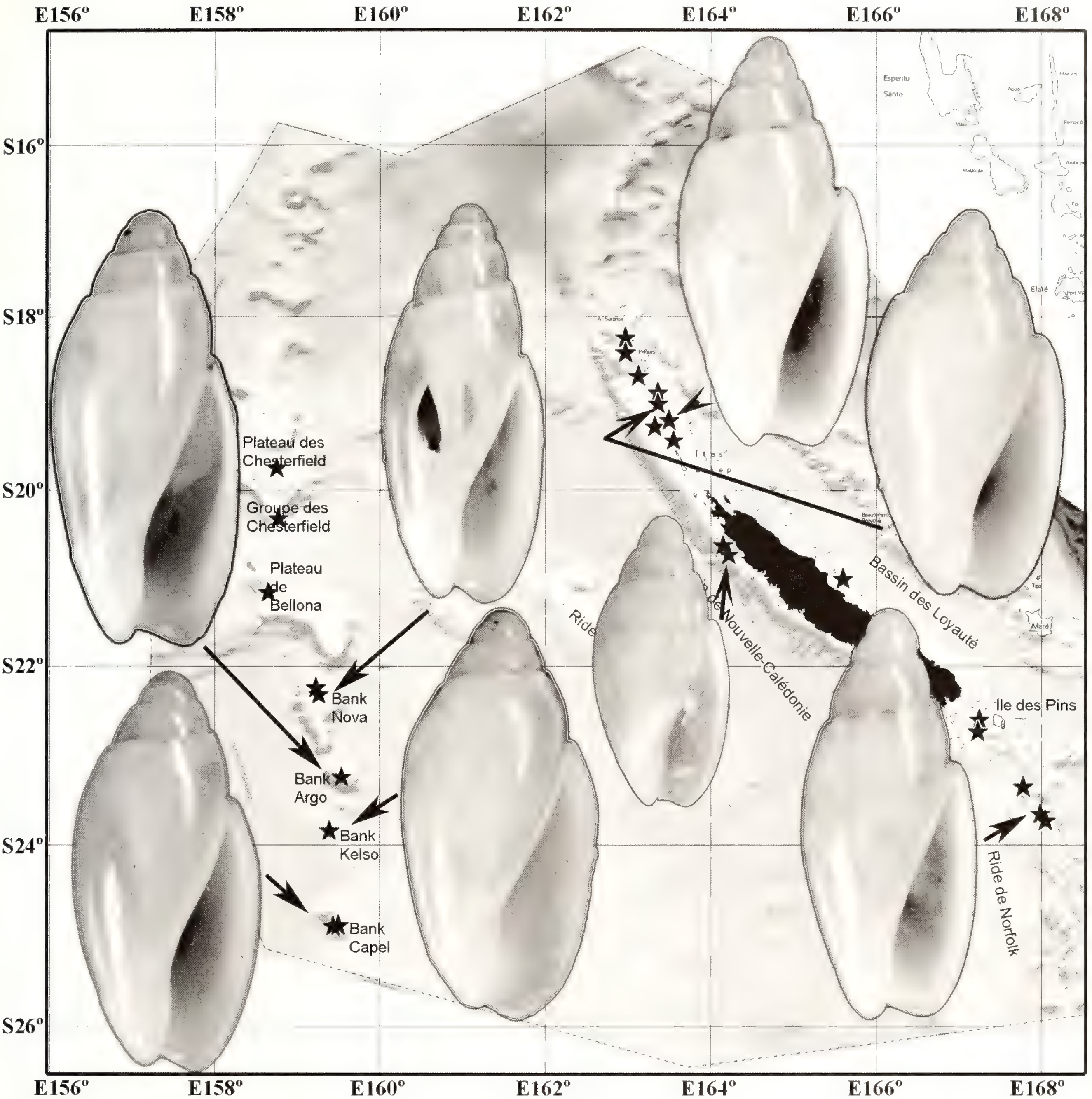
Foot with well developed parapodia and crescent-shaped propodium. Operculum present. Mantle without filament, mantle lobe well developed. Head consisting of two separate vertical flaps, separated by furrow; eyes present or absent. Rhynchostome opening situated below the right flap. Proboscis short. Salivary glands paired, accessory salivary gland absent, valve of Leiblein large, gland of Leiblein narrow tubular, stomach with long posterior mixing area. Rachidian radular teeth with 3 main cusps, central cusp narrower and shorter, additional smaller cusp abutting each side of main lateral cusps. Lateral teeth with subtriangular bases and long curved hook-like cusps.

Type species

Calyptoliva bolis Kantor and Bouchet sp. nov.

Remarks

Calyptoliva gen. nov. bears a strong overall resemblance to *Belloliva*, both in protoconch and teleoconch shape, with similar soft body gross morphology and similar radula. *Calyptoliva* differs from *Belloliva* in the absence of open filament channel of the shell, and, correspondingly, of the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Esperitu
Santo
Malakula
Efaté
A. Surprise
Huon
Pelagos
Beautemps-Beaupré
Plateau des Chesterfield
Groupe des Chesterfield
Plateau de Bellona
Bank Nova
Bank Argo
Bank Kelso
Bank Capel
Ride de Nouvelle-Calédonie
Bassin des Loyauté
Maré
Ile des Pins
Ride de Norfolk

Figure 26. Distribution of different forms of *Belloliva exquisita* (Angas, 1871) in the Coral Sea and New Caledonia.

mantle filament; it also has a mantle lobe that is not present in *Belloliva*. The gland of Leiblein is massive in *Belloliva*, tubular in *Calyptoliva*.

The mophology of the suture requires special comments. In all but one specimen studied, the suture is concealed by a very thin callus, extending slightly adapically onto the preceding whorl, and there is no filament channel. However, a specimen with corroded suture area (Fig. 27G) shows that a filament channel remains present below the callus.

Etymology

From the Greek *kalypto*, meaning to cover, to conceal, referring to the concealed filament channel of the shell.

Calyptoliva bolis Kantor and Bouchet sp. nov. (Figs. 27A-C, 28, 29)

Type material

Holotype (Moll 9480) in MNHN.

Material examined

Coral Sea, Lansdowne-Fairway Bank, CORAIL 2, st. DE14, 21°01′S, 160°57′E, 650-660 m (1 dd). MUSORSTOM 5, st. 390, 21°01′S, 160°50′E, 745-825 m (1 lv).

Type locality

Coral Sea, Lansdowne-Fairway Bank, 21°01′S, 160°57′E, 650-660 m (CORAIL 2, st. DE14).

Description (holotype)

Shell solid, glossy, elongate-oval (BWL/SL = 0.71, AL/SL = 0.54, D/SL = 0.38), with narrow aperture and high spire, consisting of just over one protoconch and 3.75 teleoconch whorls. Protoconch large, low, evenly rounded, diameter 1650 μm, exposed height 780 μm, smooth, protoconch-teleoconch transition indistinctly marked by the appearance of the callus overlapping the suture on teleoconch whorls. Profile of whorls moderately convex, evenly rounded. Suture shallowly impressed and overlain by very narrow and thin smooth callus, extending slightly adapically. Filament channel (seen by transparency through callus) narrow, closed by overlaid callus but not filled. Aperture narrow, gradually tapering adapically. Outer lip evenly and slightly convex. Parietal plate narrow, microshagreened, broadening and thickening in its abapical part prior to anterior band. Anterior plating without any plicae, similarly microshagreened except for most abapical part. Color very light yellow, anterior band white.

Dimensions (holotype largest specimen): SL 12.9 mm, SW 4.9 mm, BWL 9.2 mm, AL 7.0 mm.

Anatomy

General morphology.—Body only partially retrieved from shell, in alcohol uniformly off-white, lacking pigmentation. Mantle cavity spanning about 0.3 whorls, nephridium 0.25 whorls with transparent walls, with 8 low excretory lamellae. Anterior lobe of digestive gland small, spanning about ¼ whorl and completely separated from posterior lobe by stomach, which is oriented obliquely with regard to columellar axis. Foot thick, strongly contracted, transversely folded, metapodium broadly oval, propodium small in comparison with metapodium, typically crescent-shaped, subdivided longitudinally. Operculum transparent, very thin, elongate, constricted in upper part, without pronounced growth lines. Head poorly distinguished from the rest of the body, with two small vertical flaps (Fig. 28C). No eyes.

Mantle cavity.—Mantle edge even, forming a long, rather muscular and thicker extension on the right side, terminating with a medium-sized posterior mantle lobe (Fig. 28B, E, ml). Mantle thin, osphradium and ctenidium showing through. Siphon short, thin-walled, slightly extending beyond mantle edge (Fig. 28E), with smooth edges. Osphradium bipectinate, broad, exceeding the width of the ctenidium and about 0.8 of its length. Osphradium nearly bilaterally symmetrical, with very narrow axis. Ctenidium occupying about 0.8 of mantle length, consisting of tall triangular lamellae, similar in shape and size along most of its length, except near mantle edge where ctenidium sharply narrows and lamellae become much lower. Hypobranchial gland moderately glandular, although not forming distinct folds. Mantle filament and posterior mantle tentacle absent.

Female pallial gonoduct large, swollen, not studied in detail due to poor fixation. Female genital opening situated close to anus.

Alimentary system.—Rhynchostome asymmetrical, situated below the right cephalic flap (Fig. 28C, rns). Organs of the anterior hemocoel very contracted, compact and situated nearly at right angle with regard to pedal axis. Proboscis short in contracted state (Fig. 28D, pr), about 1.2 mm in length (0.16 AL), thick (L/W approximately 2), occupying nearly the entire rhynchocoel length, rhynchodeum thin-walled, semi-transparent. Pair of thin retractor muscles attached to median part of the rhynchodeum (wall of proboscis sheath) in retracted condition. Large odontophoral retractor extends from proboscis posteriorly, then follows anteriorly along ventral side of rhynchodeum and, bypassing the nerve ring, attached to the ventral side of cephalic hemocoel. Esophagus, posterior to proboscis, rather broad and not forming a loop. Odontophore rather broad, occupying nearly entire volume of proboscis, about the same length as proboscis and not protruding from the rear of it. Subradular cartilages large, fused antero-ventrally by rather thin interconnection. Radular sac slightly longer than the odontophore. Radula (Fig. 29) consisting of about 45 rows of teeth, width of the membrane about 155 μm (1.23% SL, 2.02% AL). Rachidian with 3 main cusps, central cusp about three times as narrow and 1.5 times shorter than lateral cusps, and an additional very small, but distinct, cusp abutting outer side of main lateral cusps. Dorsal grooves on main lateral cusps shallow and broad, best seen in lateral view (Fig. 29C). Anterior profile of rachidian nearly straight, very slightly concave in the middle. Posterior edge of basal plate very slightly convex. Sides of basal plate gradually embedded in the membrane without distinct border. Lateral teeth subtriangular with curved hook-like tips (Fig. 29D). Valve of Leiblein very large, pyriform, well distinguished from

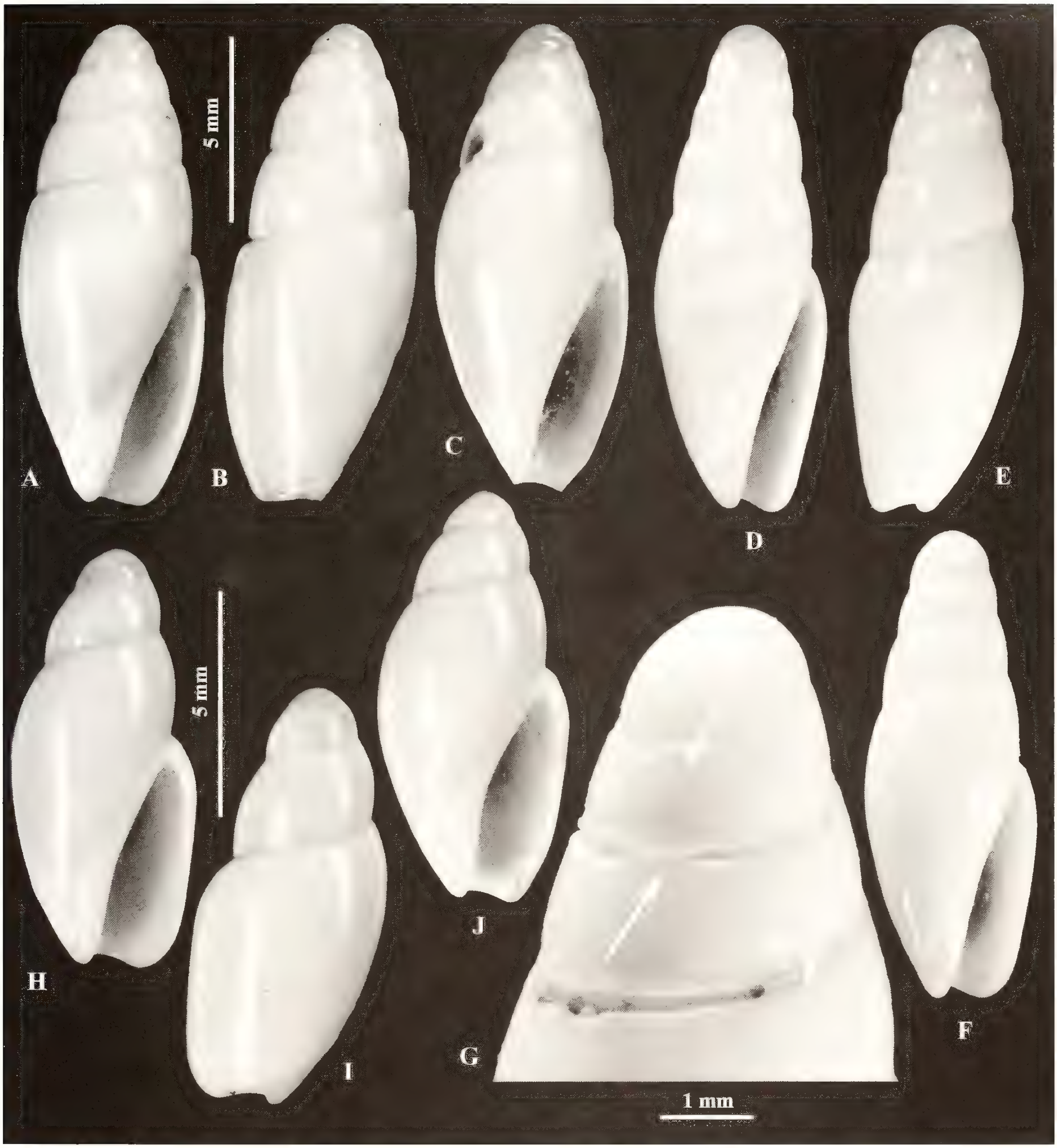

Figure 27. *Calyptoliva bolis* sp. nov. (A-C). A-B, Holotype, SL 12.9 mm. C, MUSORSTOM 5, st. 390, SL 12.6 mm. *Calyptoliva tatyanae* sp. nov. (D-G). D-E, Holotype, SL 13.1 mm. F, Paratype, SL 12.8 mm. G, Upper whorls of paratype, SL 13.0 mm, illustrating the open filament channel, covered by the callus; the areas with intact callus are indicated by white arrows. *Calyptoliva amblys* sp. nov. (H-J). H-I, Holotype, SL 9.3 mm. J, Paratype, SL 9.2 mm.

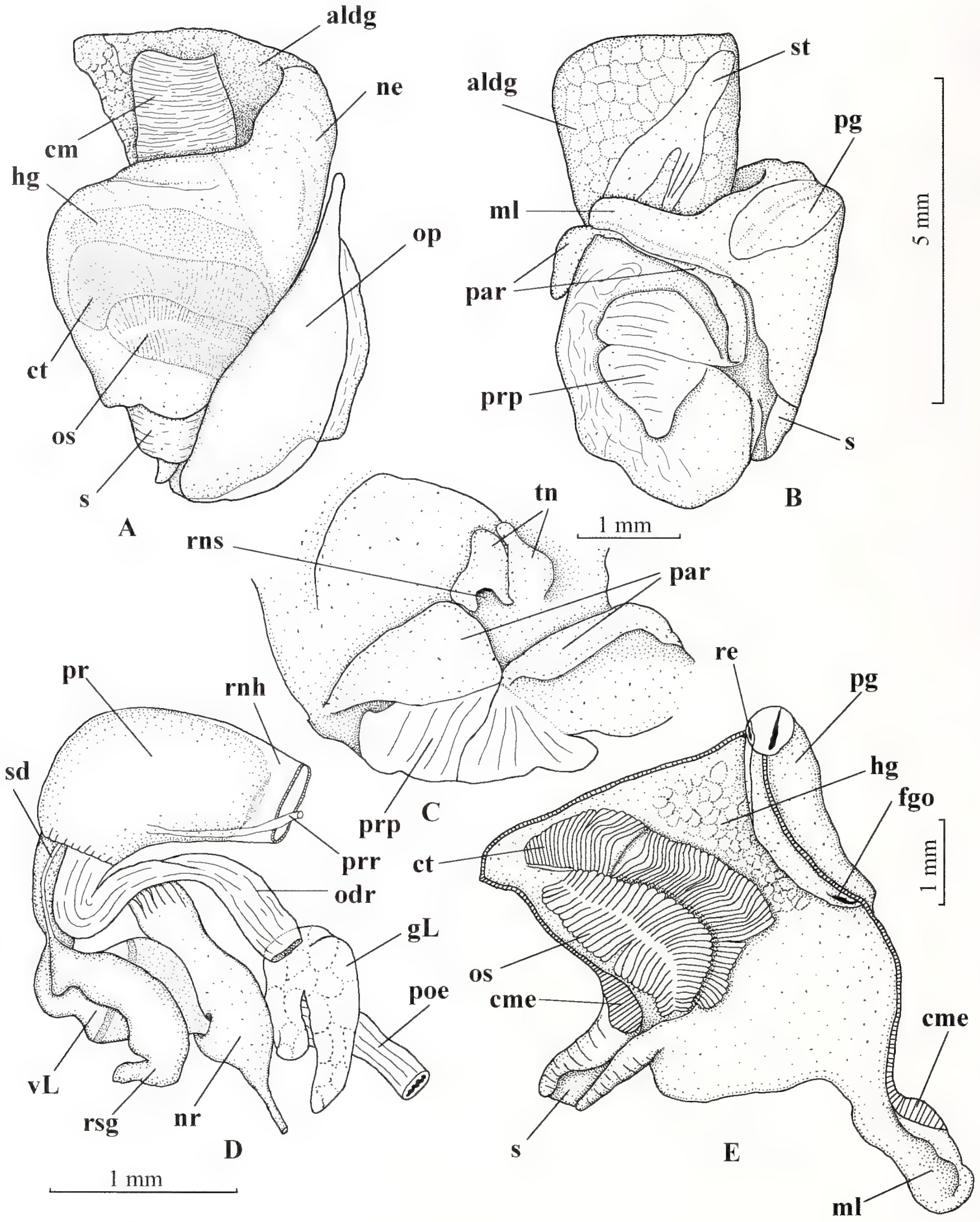
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Figure 28. Morphology of *Calyptoliva bolis* sp. nov. (for shell see Fig. 26D). A, B, Dorsal and ventral views of the body removed from the shell, respectively. C, Head-foot, anterior view, mantle and visceral mass removed. D, Right view of the anterior foregut. E, Mantle complex. Abbreviations: aldg, anterior lobe of digestive gland; cm, columellar muscle; cme, cut mantle edge; ct, ctenidium; fgo, female genital opening; gL, gland of Leiblein; hg, hypobranchial gland; ml, mantle lobe; ne, nephridium; nr, circumesophageal nerve ring; odr, odontophoral retractor; op, operculum; os, osphradium; par, parapodium; pg, pallial gonoduct; poe, posterior esophagus; pr, proboscis; prp, propodium; prr, proboscis retractor; re, rectum; rnh, rhynchodeum (= proboscis sheath); rns, rhynchostome; rsg, right salivary gland; s, siphon; sd, salivary duct; st, stomach; tn, cephalic tentacles; vL, valve of Leiblein.

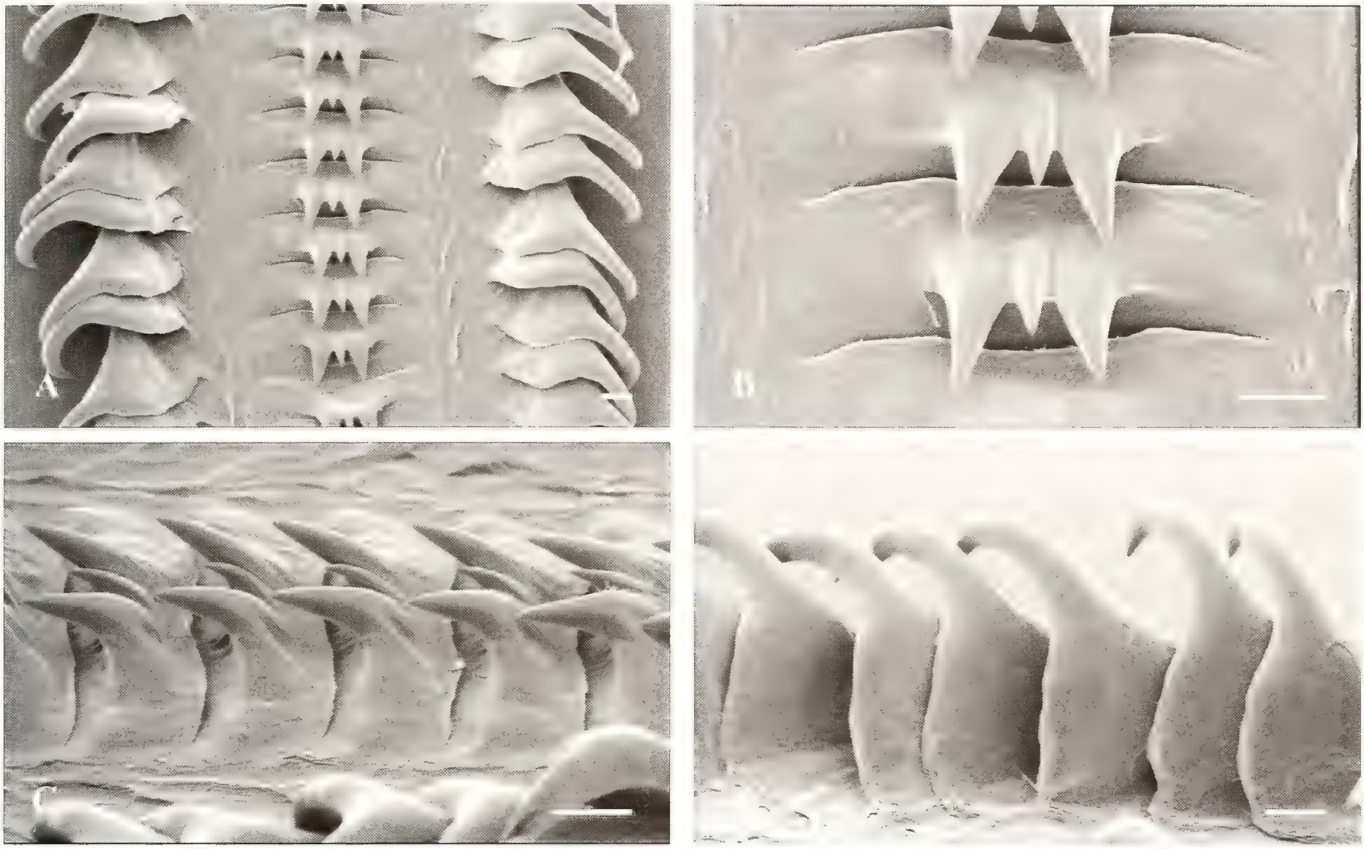


Figure 29. Scanning electron micrographs of the radula of *Calyptoliva bolis* sp. nov. A, Dorsal view of the central portion of the radular ribbon. B, Enlarged dorsal view of the rachidian teeth. C, Left lateral view of the rachidian teeth. D, Left lateral view of the lateral teeth. Scale bars = 10 µm.

esophagus (Fig. 28D, vL), which becomes very narrow immediately posterior to the valve and passes through the nerve ring.

Circumesophageal nerve ring comparatively large. Gland of Leiblein small, colorless, narrow, tubular. Opening of the duct into esophagus not traced during dissection. Salivary glands medium-sized, apparently (but not certainly due to small size) broad-tubular, left one slightly smaller than right, situated on either side of esophagus posterior to the proboscis and not fusing. Salivary ducts rather thick, entering the esophageal walls shortly after leaving the glands and passing towards their opening along esophagus dorsal side. Accessory salivary glands not found. Stomach large, spanning about 0.3 whorls, with long and narrow posterior mixing area (Fig. 28B, st). Stomach anatomy not studied in detail due to poor fixation.

Remarks

The second specimen is very similar to the holotype, except that its apertural lip is not thickened and its color is pure white.

Etymology

From the Greek *bolis*, a missile, with reference to the general shell profile; used as a noun in apposition.

Calyptoliva tatyanae Kantor and Bouchet sp. nov.
(Fig. 27D-G)

Type material

Holotype (Moll 9481) and 2 paratypes (Moll 9482) in MNHN.

Material examined

Coral Sea, Fairway Bank. EBISCO, st. CP2647, 21°32′S, 162°27′E, 737 m (3 dd).

Type locality

Coral Sea, southeastern part of Fairway Bank, 21°32′S, 162°27′E, 737 m (EBISCO, st. CP2647).

Description (holotype)

Shell solid, glossy, elongate, nearly biconic (BWL/SL = 0.61, AL/SL = 0.50, D/SL = 0.35), with narrow aperture and
]

high spire, consisting of about 0.8 protoconch and 4.75 teleoconch whorls. Protoconch very large, tall, globular evenly rounded, diameter 2340 µm, exposed height 1640 µm, smooth, protoconch-teleoconch transition indistinctly marked by the appearance of the callus overlapping the suture on teleoconch whorls. Profile of whorls weakly convex, evenly rounded. Suture shallowly impressed and overlain by very narrow and thin smooth callus, extending slightly adapically. Filament channel (seen by transparency through callus) narrow, closed by overlaid callus but not filled. Aperture narrow, tapering adapically. Outer lip slightly convex adapically and nearly straight along most of its length. Parietal plate narrow, clearly microshagreened, broadening and thickening in its abapical part prior to anterior band. Anterior plating without any plicae, similarly microshagreened. Color uniformly off-white, sutures slightly darker than the rest of the shell surface.

Dimensions (holotype, largest specimen): SL 13.1 mm, SW 4.6 mm, BWL 8.1 mm, AL 6.6 mm.

Remarks

Calyptoliva tatyanae sp. nov. differs from *Calyptoliva bolis* sp. nov. by its narrower shell with taller spire, less convex whorls, narrower aperture, and much larger protoconch (diameter 2340 µm versus 1650 µm in *C. bolis*). All three specimens are very similar in shape, with some variance in the convexity of the whorls.

Etymology

The species is named after the biologist and wife of the senior author, Tatiana Steyker, from the P.P. Shirshov Institute of Oceanology of the Russian Academy of Sciences.

Calyptoliva amblys Kantor and Bouchet sp. nov.
(Fig. 27H-J)

Type material

Holotype in AMS, 2 paratypes in MNHN.

Material examined

Coral Sea, CORAIL2, Mellish Reef, st. DW172, 18°26′S, 155°12′E, 1100 m (4 dd).

Type locality

Coral Sea, Mellish Reef, 18°26′S, 155°12′E, 1100 m (CORAIL 2, st. DW172).

Description (holotype)

Shell solid, glossy, elongate-oval, white (BWL/SL = 0.78, AL/SL = 0.54, D/SL = 0.46), with medium-wide aperture and low spire. Shell consists of 0.75 whorl of protoconch and 2.75 teleoconch whorls. Protoconch large, low, evenly rounded, diameter 1330 µm, exposed height 590 µm, smooth, protoconch-teleoconch transition is indistinctly marked by the appearance of the callus overlapping the suture on teleoconch whorls. Profile of whorls moderately convex, evenly rounded.

Suture is shallowly impressed and overlain by very narrow, thin smooth callus, extending slightly adsuturally. Filament channel (seen by transparency through callus) narrow, closed by overlaid callus but not filled. Aperture medium wide, obtuse adapically. Outer lip thickened, convex adapically, nearly straight along most of the length and rounded abapically. Parietal plate narrow, slightly broadens in its abapical part prior to anterior band, microshagreened. Anterior plating smooth, similarly microshagreened.

Dimensions (holotype largest specimen): SL 9.2 mm, SW 4.2 mm, BWL 7.2 mm, AL 5.0 mm.

Animal unknown.

Remarks

Calyptoliva amblys differs from *Calyptoliva bolis* sp. nov. by its smaller adult size with more convex whorls, wider aperture with straight lip in its middle part, and smaller protoconch. All four known specimens are very similar in shape, with some variance in the convexity of the whorls.

Etymology

From the Greek *amblys*, obtuse, with reference to the shell shape.

DISCUSSION

Revised diagnosis of *Belloliva*

Iredale (1924) described *Gemmoliva* as a subgenus of *Belloliva*, with *Olivella pardalis* A. Adams and Angas, 1864 as type species, based on minor differences in radulae (Peile 1922) namely the additional marginal cusps on the rachidian tooth were said to be "very small and apparently sometimes missing." We found this character to be of not more than specific value in the species of *Belloliva* we studied and, the shell and anatomical characters being otherwise equal, we agree with Wilson (1994) in synonymizing *Gemmoliva* with *Belloliva*. Thiele (1929 in 1929-1931) also described *Olivellopsis* as a subgenus of *Belloliva*, with *Olivella simplex* Pease, 1868 as type species based on subtle shell differences (essentially suture more appressed and columellar callus without lower fold). However, its radula and gross morphology do not differ significantly from other species of *Belloliva*, including its type species, and thus do not support segregation of *O. simplex* in a separate genus-group taxon.

As a result of the new data presented in this paper and comparison with other taxa, the following is a revised diagnosis of *Belloliva*.

Shell less than 15 mm long, olivelliform, elongate-oval, with attenuated spire, and open filament channel. Protoconch paucispiral, consisting of about one whorl or less, smooth, evenly rounded, large in comparison with the teleoconch, diameter 1000-1800 µm, protoconch-teleoconch transition marked by the onset of filament channel. Aperture elongate or lanceolate-oval, gradually narrowing abapically. Parietal plate narrow, slightly thickened, anterior plating smooth or plicate. Foot with well developed parapodia and crescent-shaped propodium. Operculum usually present, narrow. Mantle with mantle filament, without mantle lobe. Head with two separate vertical flaps, separated by furrow. Rhynchostome opening below the right flap. Proboscis short or of medium length when retracted. Salivary glands paired, ramified tubular, accessory salivary glands absent, valve of Leiblein medium-sized to large, gland of Leiblein bulky, stomach with long posterior mixing area. Rachidian radular teeth with 3 main cusps, central cusp narrower and shorter than the lateral ones, and additional small, but usually distinct, cusps abutting each side of the main lateral cusps. Lateral teeth with subrectangular or subtriangular bases and long curved hook-like cusps.

Composition of the genera

Four Australian species have traditionally been included in *Belloliva* (Kaicher 1987, Wilson 1994, see below). In addition, a couple of other taxa have been, at one time or another, allocated to the genus and need to be discussed separately.

(1) Based on his examination of the radula of *Olivella tabulata* Dall, 1889 from off Cuba, Olsson (1956) tentatively included it in *Belloliva*, and this placement was followed by Kaicher (1987). We concur with Olsson that *Olivella tabulata* bears an overall resemblance to *Belloliva*, especially in the large size of the protoconch. However, Olsson described the radula with a rachidian bearing 3 cusps, of which the central one is the largest, whereas in *Belloliva* from Australia (including the type species) and the South-West Pacific, the central cusp is the smallest. In addition, *O. tabulata* lacks an operculum (Dall 1889), a character admittedly shared with *Belloliva apoma* but with no other species of *Belloliva*. The diverging distributions and the radular differences suggest that *O. tabulata* is probably not congeneric with the Australia-South-West Pacific clade, but probably belongs to some other, possibly still unnamed, genus of the subfamily Olivinae.

(2) Hunon (2000) attributed *Oliva lacanientai* Greifeneder and Blöcher, 1985 to *Belloliva* based on the presence of two fasciolar bands and protoconch shape; Hunon also stated he had found remains of an operculum. We have examined material of *O. lacanientai* and find Hunon's statement misleading, since shell shape and protoconch (multispiral, consisting of about 4.25 whorls) are typical for *Oliva*. Examination of the anatomy and radula (Fig. 30A) confirm a placement in *Oliva*. We did not find an operculum and we suggest that Hunon mistakenly interpreted the presence of an operculum from the presumably rotten and dried (as this was dealer's material from tangle nets) soft parts of his specimen.

The present study thus brings to 10 the number of species included in *Belloliva*, and three in *Calyptoliva*, and highlights the Coral Sea as their center of diversity: In fact, our material still contains one additional undescribed species from Lansdowne-Fairway Banks (represented by a single empty juvenile shell), suggesting that additional findings of new species of *Belloliva* in the Coral Sea are still possible. By contrast, it should be emphasized that cruises conducted since 1992 in other South Pacific archipelagoes (Solomons, Vanuatu, Fiji, Wallis and Futuna, Tonga, Marquesas) did not yield any deep-water material of *Belloliva* or *Calyptoliva*.

Thus the following species are currently recognized: *Belloliva alaos* sp. nov., northern New Caledonia, alive in 668 m, shells in 397-660 m (Fig. 31), *Belloliva apoma* sp. nov., northern New Caledonia, alive in 502-516 m, shells in 470-550 m (Fig. 31), *Belloliva brazieri* (Angas, 1877), type species of the genus, coastal waters of south-eastern Australia (New South Wales, Victoria, and Tasmania) (Fig. 32A-B), *Belloliva dorcas* sp. nov., Coral Sea, Chesterfield Plateau and Lansdowne-Fairway Bank, shells in 230-355 m (Fig. 31), *Belloliva ellenae* sp. nov., Coral Sea, Chesterfield plateau, alive in 386-486 m (Fig. 31), *Belloliva exquisita* (Angas, 1871), coastal waters of eastern Australia, Coral Sea and New Caledonia, alive in 26-345 m (Fig. 31), *Belloliva leucozona* (A. Adams and Angas, 1864), coastal waters of the eastern seaboard of Australia from Caloundra, Queensland to Lorne, Victoria (Fig. 32C-D), *Belloliva obeon* sp. nov., Coral Sea, Chesterfield Plateau and Lansdowne-Fairway Bank, alive in 500-672 m, shells from 252 m (Fig. 31), *Belloliva simplex* (Pease, 1868), coastal waters of Tuamotu Island (French Polynesia), Samoa, Tonga, Loyalty Islands, New Caledonia, and Vanuatu, alive in 10-45 m (Fig 31), *Belloliva triticea* (Duclos, 1835) (= *O. pardalis* A. Adams and Angas, 1864), coastal waters of southern Australia (New South Wales to Albany, Western Australia) (Fig. 32E-F), *Calyptoliva amblys* sp. nov., Coral Sea, Mellish Reef, shells in 1100 m, *Calyptoliva bolis* sp. nov., Coral Sea, Lansdowne-Fairway Bank, alive in 745-825 m, shells from 650-660 m (Fig. 31), *Calyptoliva tatyanae* sp. nov., Coral Sea, Fairway Bank, shells in 737 m (Fig. 31).

All species of *Belloliva* and *Calyptoliva* have a paucispiral protoconch indicating non-planktotrophic development, and therefore inferred limited larval dispersal, which probably account for restricted ranges and multiple speciation

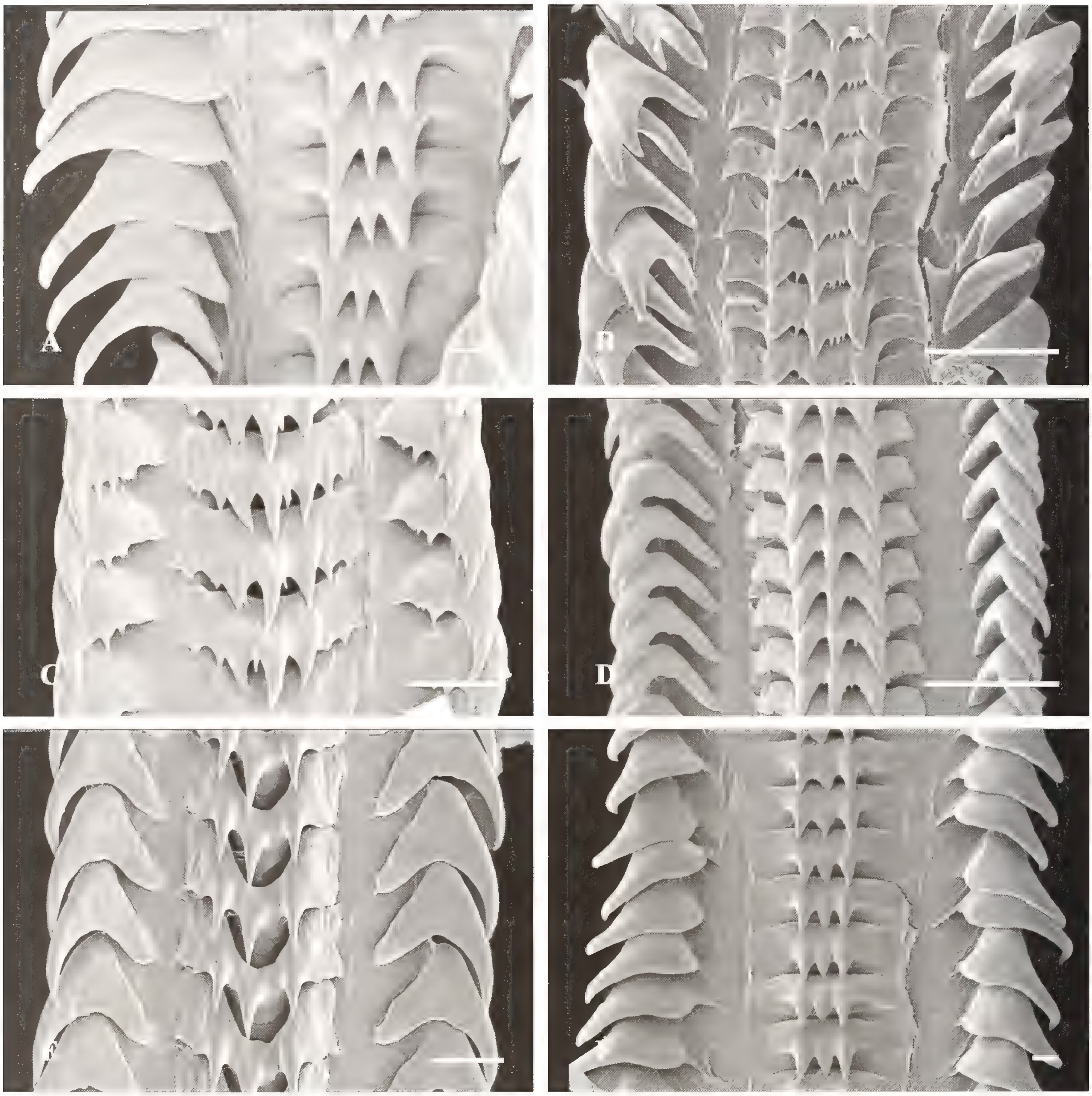
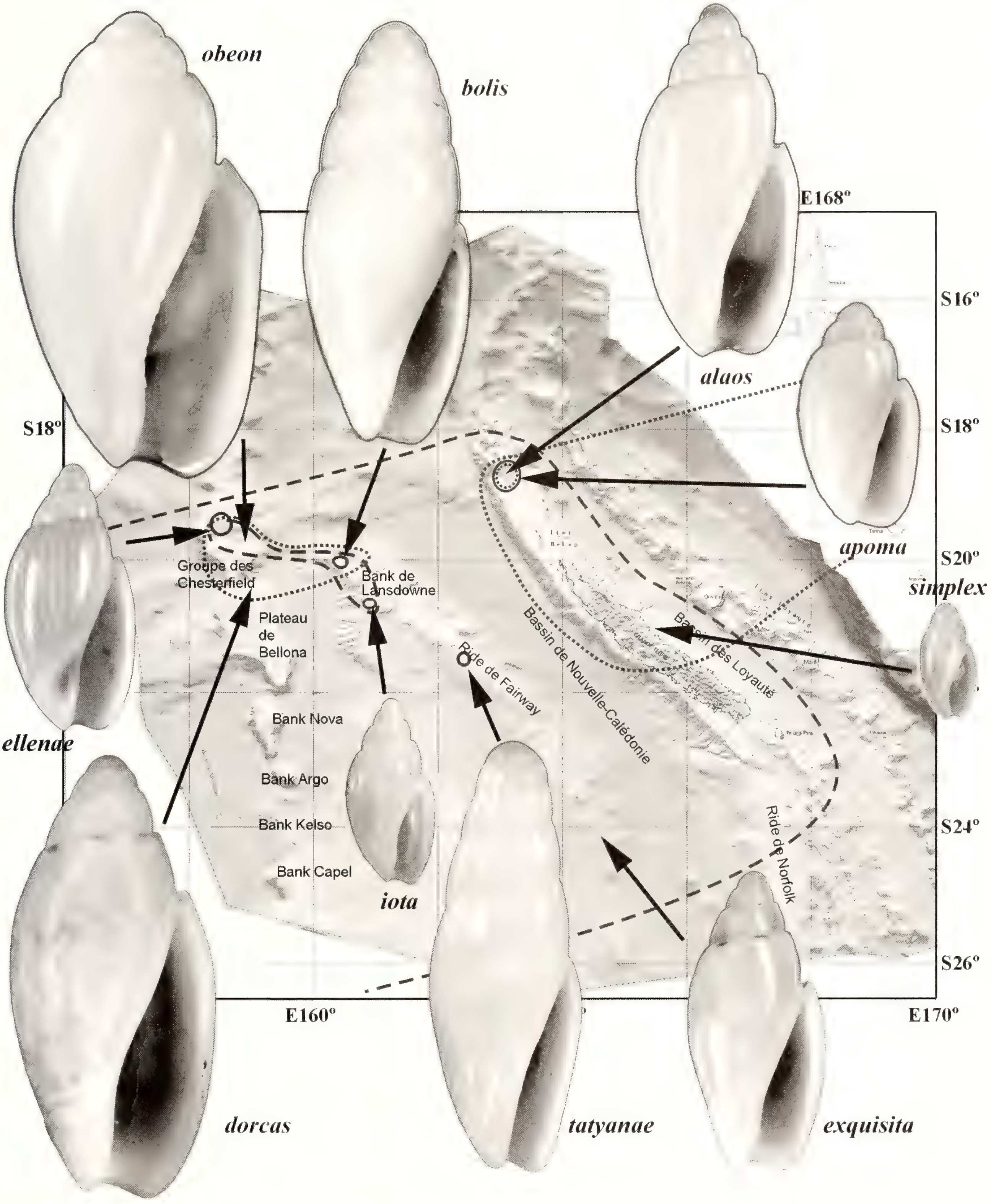


Figure 30. Scanning electron micrographs of the radulae of different members of Olividae. A, *Oliva lacanientai* Greifeneder and Blöcher, 1985 (Coral Sea, MUSORSTOM 5, sta. 380). B, *Ancila cinnamomea* Lamarck, 1801 (Southern India, Rameshwaran). C, *Ancillina* sp. (northern New Caledonia, BATHUS 4, st. DW914). D, *Amalda fuscolingua* Kilburn and Bouchet, 1988 (northern New Caledonia, BATHUS 2, st. DW729). E, *Turrancila* sp. (Indonesia, KARUBAR, st. CP71). F, *Belloliva alaos* sp. nov. (northern New Caledonia, MUSORSTOM 4, st. DW160). Scale bars = 10 μm (A, C, E, F), 100 μm (B, D).

events on the isolated seamounts and banks in the middle of the Coral Sea. However, it is difficult to ascertain whether the very narrow ranges of some of the new species are real or represent sampling artefacts. For instance, *Belloliva ellenae* is known from 8 stations that straddle only 30 km on the Chesterfield Plateau (Fig. 31), and *Belloliva apoma* is known from 4 stations over a distance of 35 km. Conversely, *Belloliva exquisita* ranges from Australia to New Caledonia, including isolated guyots and banks in the Coral Sea. Limited sampling in the Coral Sea may explain the apparently extremely narrow ranges, such as that of *B. ellenae*, but the more than one thousand hauls taken in New Caledonia suggest that the very limited range of *B. apoma* is real. A similar pattern of narrow endemism has been de-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alaos
E168°
S16°
S18°
S18°
apoma
S20°
simplex
ellenae
Groupe des Chesterfield
Bank de Lansdowne
Plateau de Bellona
Ride de Fairway
Bassin de Nouvelle-Calédonie
Bassin des Loyauté
Bank Nova
Bank Argo
Bank Kelso
Bank Capel
iota
Ride de Norfolk
S24°
S26°
E160°
E170°
dorcas
tatyanae
exquisita

Figure 31. General distributions of Coral Sea and New Caledonian species of *Belloliva* and *Calyptoliva.* Holotypes illustrated when named in this paper, all at the same scale.

scribed in the family Volutomitridae (Bouchet and Kantor 2004).

Position of *Belloliva* and *Calyptoliva* in the family Olividae

Although the genus *Belloliva* has been referred to Olivellidae (or Olivelliinae) in the recent literature (e.g., by Wilson 1994, Tursch and Greifeneder 2001, Sterba 2003), this is not supported by its radular morphology, a point already made by Olsson (1956), who referred the genus to the Olivinae. The current consensus (Bouchet and Rocroi 2005) on the composition and classification of the family Olividae is to recognize two subfamilies, the nominal subfamily Olivinae (synonyms Agaroniinae and Olivancillariinae) and the Ancillariinae (= Ancillinae). Surprisingly few anatomical data are available, essentially only for various species of *Oliva* (Marcus and Marcus 1959, Kantor 1991, Kantor and Tursch 2001) and two of *Olivancillaria* (Marcus and Marcus 1959); for Ancillariinae, the information is restricted to just two species of *Amalda* (Marcus and Marcus 1968, Kantor 1991).

One of the characteristic traits of the family Olividae is the presence of mantle appendages. The most complex assemblage is present in the Olivinae, which have anterior mantle tentacle, a mantle filament, and a mantle lobe. The mantle filament is a muscular, contractile, and mobile organ which originates on the right side of the mantle edge, extending through the aperture adapically and positioning in the filament channel. It is present in all oliviform gastropods (including the Olivellidae) that have channelled sutures, and its function remains unknown. The anterior mantle tentacle is situated near the siphon and, when the snail is crawling, it passes through the siphonal canal and rests on the dorsal side of the shell. Its function is not known either. The small posterior mantle lobe is situated at the base of the mantle filament (when present). In *Belloliva*, only a rather short (in preserved animals) mantle filament is present; neither an anterior mantle tentacle nor a mantle lobe were found in dissections. By contrast, in *Calyptoliva*, the mantle filament is absent but the mantle lobe is well-developed. Judging from the differences in shell morphology, it may be inferred that the mantle lobe is responsible for secreting the primary spire callus (following the terminology of Kilburn 1977) that overlies the suture, rather than producing the columellar callus (as suggested by Marcus and Marcus 1959), which is equally developed in the two genera.

With the Olivinae *Belloliva* shares a canaliculate suture

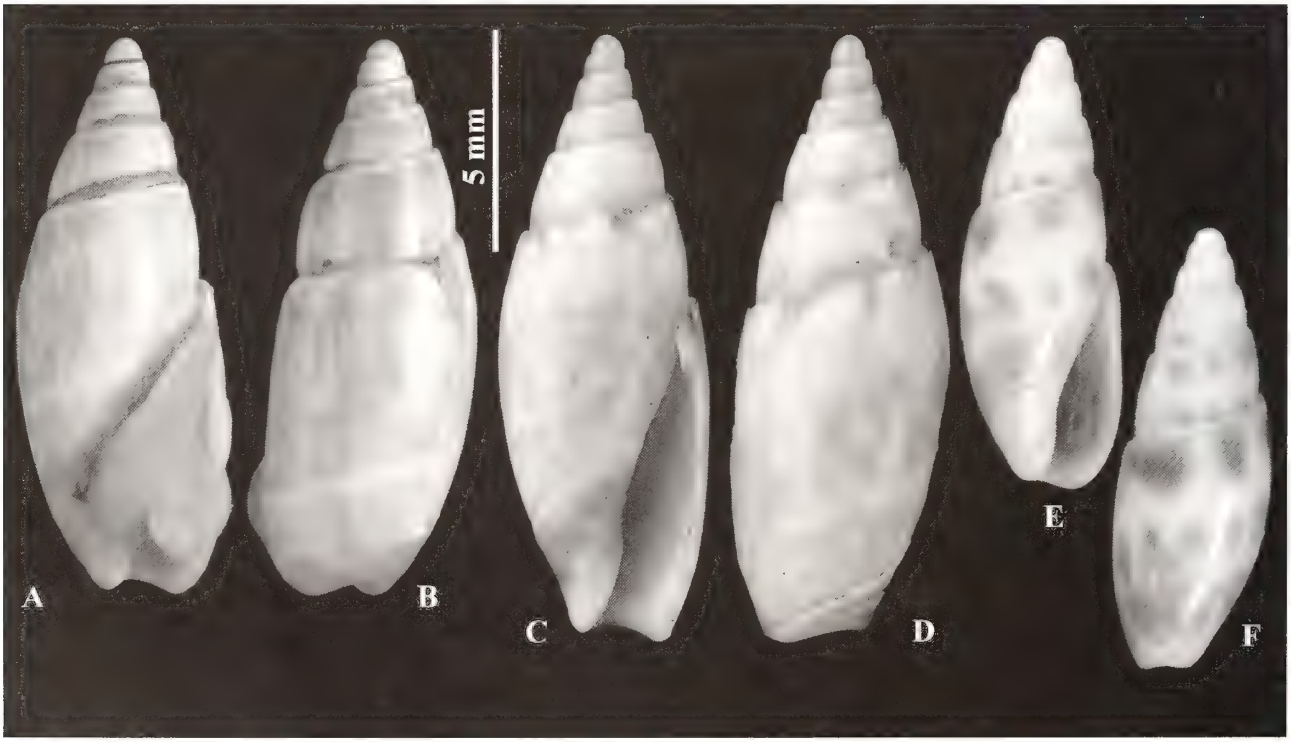

Figure 32. A-B, *Belloliva brazieri* (Angas, 1877), AMS C388726, dissected specimen (SL 12.9 mm). C-D, *Belloliva leucozona* (A. Adams and Angas, 1864), probably illustrated syntype, BMNH 1870.10.26.93 (SL 13.8 mm). E-F, *Belloliva triticea* (Duclos, 1835), illustrated syntype, MNHN 1273 (SL 10.6 mm), photo by D. Brabant.

and, correspondingly, the presence of a mantle filament, a foot that is rounded posteriorly, a stomach that has a long posterior mixing area, and the radula type. The olivine radula is rather uniform (Troschel 1866, Marcus and Marcus 1959, Kantor and Tursch 2001), with rachidians with 3 non-serrated cusps and laterals that are leaf-shaped, concave posteriorly, and convex anteriorly with long curved hook-like tips (Fig. 30A). However, *Belloliva* (and *Calyptoliva*) differs from all Olivinae in having an operculum; it also differs from *Oliva* in the absence of the anterior mantle tentacle (which is also absent in *Olivancillaria*) and mantle lobe. The absence of tentacles on the vertical flaps on the head of *Belloliva* and *Calyptoliva* is a character shared with *Olivancillaria*, but not with *Oliva*. *Calyptoliva* differs from Olivinae in its open filament channel overlain by thin callus; superficial examination of two ancillariines (*Entomoliva mirabilis* Bouchet and Kilburn, 1991 and *Amalda aureomarginata* Kilburn and Bouchet, 1988) revealed complex multi-layered structure of the shell but no sign of the filament channel. At this moment we do not know whether the peculiar suture of *Calyptoliva* should be regarded as ancestral (representing an intermediate stage between Olivinae and Ancillariinae), or an autapomorphy of *Calyptoliva*.

With the Ancillariinae *Belloliva* and *Calyptoliva* share the presence of an operculum and the head morphology. *Calyptoliva* also shares with the Ancillariinae the suture covered by a thin callus. *Belloliva* differs from Ancillariinae in having a channelled suture and a mantle filament. Both *Belloliva* and *Calyptoliva* differ from Ancillariinae in a stomach with a long posterior mixing area (the only genus of Ancillariinae studied in this respect, *Amalda*, has a narrow tubular U-shaped stomach without posterior mixing area), and a rounded versus posteriorly deeply notched foot. Ancillariine radulae (Fig. 30B-E) are much more variable than those of the Olivinae and essentially follow a genus-specific pattern; rachidians are multicuspid in *Turrancilla* Martens, 1903 (Fig. 30E) and *Ancillina* Bellardi, 1882 (= *Gracilancilla* Thiele, 1925) (Fig. 30C), or have three major cusps and numerous

Table 1. Summary of major characters of Olivinae, Ancillariinae and *Belloliva* and *Calyptoliva*.

	Olivinae				Ancillariinae
Character	*Oliva**	*Olivancillaria***	*Belloliva*	*Calyptoliva*	*Amalda****
Suture of the shell	Canaliculate	Canaliculate	Canaliculate	Non-canaliculate, overlaid by callus	Non-canaliculate, overlaid by callus
Operculum	Absent	Absent	Present	Present	Present
Foot	Rounded posteriorly	Rounded posteriorly	Rounded posteriorly	Rounded posteriorly	Notched posteriorly
Head morphology	Vertical flaps with tentacles	Vertical flaps without tentacles	Vertical flaps without tentacles	Vertical flaps without tentacles	Dorso-ventrally compressed flaps without tentacles
Anterior mantle tentacle	Present	Absent	Absent	Absent	Absent
Mantle filament	Present	Present	Present	Absent	Absent
Mantle lobe	Present	Present	Absent	Present	Present
Stomach	With long posterior mixing area	?	With long posterior mixing area	With long posterior mixing area	U-shaped, without posterior mixing area
Rachidian of the radula	Tricuspid, with non-serrated cusps	3 main non-serrated cusps and additional cusps abutting each side of the main lateral cusps	3 main non-serrated cusps and additional cusps abutting each side of the main lateral cusps	3 main non-serrated cusps and additional cusps abutting each side of the main lateral cusps	3 main serrated cusps
Lateral teeth of the radula	Leaf-shaped, concave posteriorly, and convex anteriorly with long curved hook-like tips	Leaf-shaped, concave posteriorly, and convex anteriorly with long curved hook-like tips	Leaf-shaped, concave posteriorly, and convex anteriorly with long curved hook-like tips	Leaf-shaped, concave posteriorly, and convex anteriorly with long curved hook-like tips	Nearly flat, without complex, bent tips

* Data based on Marcus and Marcus (1959), Kantor (1991), and Kantor and Tursch (2001).

** Data based on Marcus and Marcus (1959).

*** Data based on Marcus and Marcus (1968), and Kantor (1991).

smaller denticles or serrations on the rachidian in *Amalda* (Fig. 30B, D). In addition, the lateral teeth of the Ancillariinae are nearly flat, without complex, bent tips. The radulae of *Belloliva* and *Calyptoliva* are therefore much closer to that of Olivinae than to that of Ancillariinae.

In conclusion, *Belloliva* and *Calyptoliva* share morphological and conchological characters with both Olivinae and Ancillariinae (Table 1). The general similarity between *Belloliva* and *Calyptoliva* in most shell characters, external anatomy, anatomy of the digestive system, and radula is remarkable, and is not likely to be the result of convergence. Thus, their differing in the presence/absence of an open canaliculate suture puts into question the validity of this character, which was hitherto considered to be a fundamental difference between, respectively, the Olivinae and Ancillariinae. Clearly, the validity of the two subfamilies requires examination of the anatomy of additional genera.

ACKNOWLEDGEMENTS

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Epibionts on *Flexopecten felipponei* (Dall, 1922), an uncommon scallop from Argentina

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Abstract: *Flexopecten felipponei* (Dall, 1922) is a non-commercial, seldom reported pectinid from the SW Atlantic Ocean. In this contribution we review its taxonomy, describe epifaunal species and their levels of encrustation, and discuss the composition of the macrobenthic assemblage where this scallop lives. Eighteen epibiont taxa were observed to live on the valves of these scallops. The most frequent and abundant epibionts on *F. felipponei* were serpulids, barnacles, and oysters. Although both valves were encrusted, the left valves had higher percentages of coverage. The benthic community contained 69 invertebrate taxa that generally characterize other mid-shelf bottoms between 37°S and 39°S. Eight pea crabs of the species *Tumidotheres maculatus* (Say, 1818) were found inside eight individuals of *F. felipponei*. Two other scallops had burrows of *Polydora websteri* Hartman, 1943. These were the first observations of these infestations on *F. felipponei*.

Key words: Epibiosis, Pectinidae, SW Atlantic Ocean

Scallops are distributed worldwide and support important commercial fisheries and mariculture efforts. They are one of the best known groups of bivalves. Numerous studies on the biology, anatomy, physiology, genetics, population dynamics, fishery, and aquaculture of commercial pectinids have been carried out (see Shumway and Parsons 1991). In Argentina, the commercial pectinids include *Aequipecten tehuelchus* (d'Orbigny, 1846) and *Zygochlamys patagonica* (King and Broderip, 1832) (Ciocco *et al.* 2006), target species of a local fishery in the gulfs of northern Patagonia (Lasta *et al.* 1998, Ciocco *et al.* 1998) and of a fishery that started in 1996 (Lasta and Bremec 1998), respectively.

During the course of cruises conducted in 2002 to locate new commercial beds of *Aequipecten tehuelchus* in the coastal shelf waters of Buenos Aires, we observed the presence of the non-commercial pectinid *Flexopecten felipponei* (Dall, 1922) as part of the benthic community. The species has rarely been recorded from the SW Atlantic Ocean (Waller 1991). It is distributed from 36°S to San Matías and Nuevo Gulfs (43°S), and has been collected in rocky and sandy bottoms from the lower tidal fringe (Castellanos 1970, 1971) and between 40 to 50 m depth (Ríos 1994, Nuñez Cortés and Narosky 1997). The only biological study on *F. felipponei* indicates that it is a simultaneous hermaphrodite (Penchaszadeh and Giménez 2001).

The availability of a suitable substratum is one of the critical factors for the colonization of sessile species. Molluscs, decapod carapaces, and the spines of sea urchins are frequently used as hard substrata available for attachment of sessile organisms in soft bottoms, together with many other organisms such as ascidians, corals, gorgonians, and sea pens that are also used as surfaces for settlement by invertebrate larvae (Abelló *et al.* 1990, Davis and White 1994, Gutt and Schickan 1998). Epibiosis is the association between epibionts (organisms growing attached to a living surface) and basibionts (organisms that provide substrate to the epibionts). This association creates a complex network of benefits and disadvantages for both organisms (Wahl 1989). Bivalves are often associated with encrusting epibionts (see Feifarek 1987, Vance 1978, Keough 1984). Epizoic organisms can be very diverse, especially on scallops (*i.e.*, Waloszek 1991, Rosso and Sanfilippo 1994, Fuller *et al.* 1998, Bremec and Lasta 2002). Studies examining the epibiosis between scallops and other organisms include foraminiferans (Alexander and Delaca 1987), sponges (Evans 1969, Bloom 1975, Forester 1979, Chernoff 1987, Burns and Bingham 2002, Donovan *et al.* 2002), hydroids (Getchell 1991), polychaetes (Blake and Evans 1973, Bergman *et al.* 1982, Mori *et al.* 1985, Ciocco 1990, Sanfilippo 1994), crustaceans (Donovan *et al.* 2003), bryozoans (Ward and Thorpe 1991), and ascidians (see Uribe *et al.* 2001 and references therein).

In this contribution we give new information about *Flexopecten felipponei* from coastal shelf waters of Buenos Aires, Argentina. We review its taxonomy, describe epifaunal species and their levels of encrustation, and discuss the composition of the macrobenthic assemblage where this scallop lives.

MATERIALS AND METHODS

Sampling was conducted with commercial otter trawls (51 hauls) by the scallopers *Atlantic Surf I*, *Erin Bruce*, and *Mr. Big*, between 40-50 m depth and between 39°00'-

39°37′S and 60°21′- 58°47′W in February, July, August, and September 2002, and with a dredge by the research vessel *Capitán Cánepa* (INIDEP) at 38°26′S and 57°40′W in January 2004 (Fig. 1). Samples of the macrobenthic community were frozen on board. The species of macroinvertebrates comprising this community were identified to the lowest possible level in the laboratory using the available literature (Bernasconi 1964, 1973, Castellanos 1970, Orensanz 1975, Fauchald 1977, Bernasconi and D'Agostino 1977, Boschi *et al.* 1992, Lana and Bremec 1994, Roux and Bremec 1996, Pérez 1999, and Forcelli 2000). The identification of ascidians was made by Dr. Marcos Tatián.

From a total of 95 specimens of *Flexopecten felipponei* identified in 26 hauls, we preserved 30 available specimens in 5% buffered formalin solution in seawater. Presence-absence and quantitative data of epibionts were recorded for right and left valves. A Wilcoxon matched paired test (Steel and Torrie 1985) was used to establish the significance in differences between total abundances of epibionts on each valve. To quantify the level of encrustation, each valve was arbitrarily divided into seven regions (Fig. 2), roughly following the procedures of Ward and Thorpe (1991) and Sanfilippo (1994). The percentage of coverage of each species of epibiont was estimated by eye as either <10%, 10-30%, or >30% of the surface for each region of each valve. Maximum shell width was measured to the nearest mm with calipers (Fig. 2).

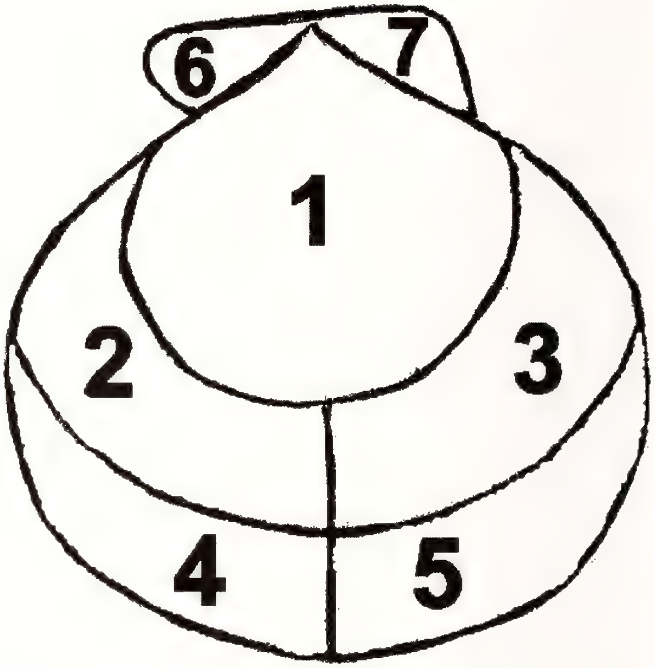

Figure 2. Diagram showing division of each valve into 7 arbitrary regions and the measurement of maximum shell width.

RESULTS

Taxonomy

Our study material agreed well with the original description of *Flexopecten felipponei* (Dall, 1922). The genus belongs to the Decatopecten group (Waller 1991) and is characterized by plain shells with 5-8 ribs that are sometimes inconspicuous. *Flexopecten felipponei* is an uncommon species from the Argentine Sea. It has been synonymized as:

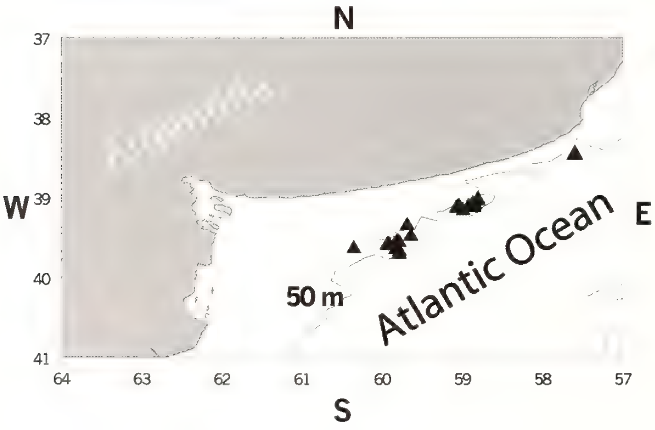

Figure 1. Map of the sampling area. Triangles mark sampling sites.

Flexopecten felipponei (Dall, 1922)

Pecten felipponei: Dall 1922; Carcelles 1944
Chlamys felipponei: Castellanos 1970,1971; Waloszek 1984; Rombouts 1991; Ríos 1994; Nuñez Cortés and Narosky 1997; Forcelli 2000
Aequipecten felipponei: Nuñez Cortés and Narosky 1997; Penchaszadeh and Giménez 2001
Flexopecten felipponei: Waller 1991; Peña 2001

We follow the nomenclature proposed by Waller (1991), who assigns the species to the genus *Flexopecten* based on the external morphology of the shell.

Epibiosis

Epibionts were present on both valves of all studied individuals of *Flexopecten felipponei.* Tube-building polychaetes, barnacles, and oysters were the most frequent epizoic organisms on both valves (Fig. 3). Significant differences were found in total number of epibionts recorded between both valves ($Z = 3.3629$, $p < 0.001$); the highest number of organisms was always found on the upper (left) valve.

Serpulid tubes were present on 90% of the sampled scallops and were found on both valves (Fig. 4). These tubes were found in all 7 regions on both valves, with variable

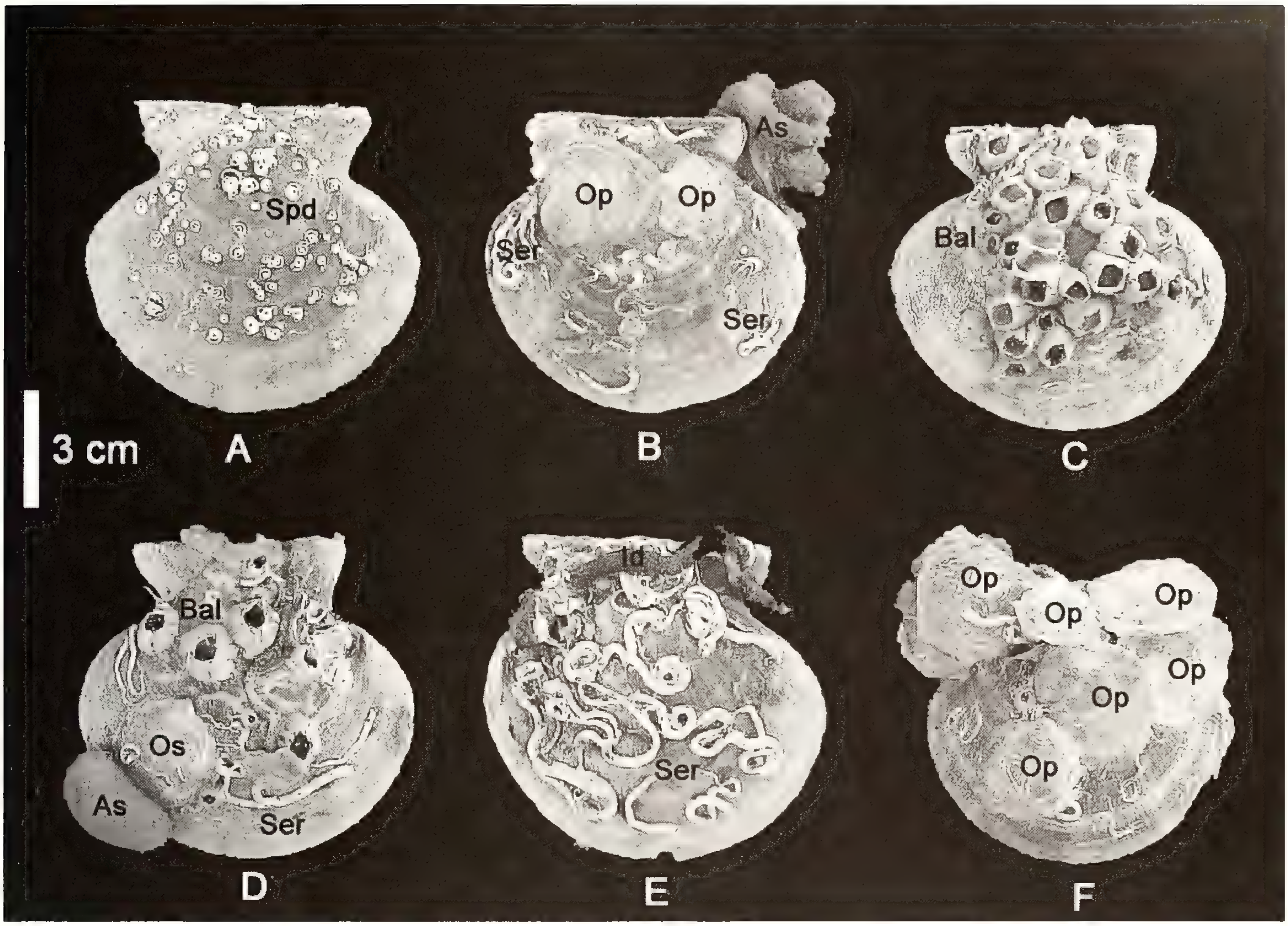

Figure 3. Epizoic organisms on *Flexopecten felipponei* from the coastal shelf waters of Buenos Aires. A, Spirorbid polychaetes. B, Several individuals of *Ostrea puelchana* d'Orbigny, 1841, ascidians, and some serpulid tubes. C, *Balanus* cf. *amphitrite*. D, *Balanus* cf. *amphitrite*, ascidians, serpulid tubes, and individuals of *Ostrea puelchana*. E, *Idanthyrsus armatus* Kinberg, 1867 (Sabellariidae) and serpulid tubes. F, *Ostrea puelchana*, some with serpulid tubes on them. Abbreviations: As, ascidian; Bal, *Balanus* cf. *amphitrite*; Ia, *Idanthyrsus armatus*; Op, *Ostrea puelchana*; Ser, Serpulid polychaetes; Spd, Spirorbid polychaetes.

percentages of covered surface in each region (Fig. 5A-B). In some cases the complete valve was covered, while in others only a few tubes were found (Fig. 3). The number of tubes found on a single valve varied between 1 and 65. Serpulids were also epibionts of other epibionts of *Flexopecten felipponei*. For example, they also occurred on epizoic individuals of *Ostrea puelchana* d'Orbigny, 1842 (Fig. 3D-F). Only 3 small individuals (<26 mm maximum height) of *F. felipponei* had valves that lacked serpulid tubes. Tubes of the polychaete *Phyllochaetopterus* sp. were found on both valves (left: 60%; right: 46.7%) (Fig. 4). These tubes were small and consequently covered small surfaces (<10%). They were found on both valves, more abundantly on the left (2-16 tubes) than on the right (1-5 tubes). Tubes of *Idanthyrsus armatus* Kinberg, 1867 were found only on left valves in 33.3% of the sampled scallops (Fig. 4). These tubes were found on the left valves in any of the 7 regions, but there was generally only one tube per valve. In some cases, the open region of the tube extended over the valve (Fig. 3E). Spirorbid tubes were very abundant on 3 (10%) scallops belonging to a particular sample (Fig. 4). In any case, they were not frequent epibionts on *F. felipponei*; only 3 scallops had between 47 and 224 tubes per valve, which were homogeneously distributed on both valves (Fig. 3A). Members of the Eunicidae (*Eunice magellanica* Mc Intosh, 1885 and *Eunice argentinensis* [Treadwell, 1929]) were recorded on only a few scallops (Fig. 4). A few burrows of the parasitic polychaete *Polydora websteri* Hartman, 1943 were found on 2 left (upper) valves (6.67%).

Barnacles (*Balanus* cf. *amphitrite*) were found on 26

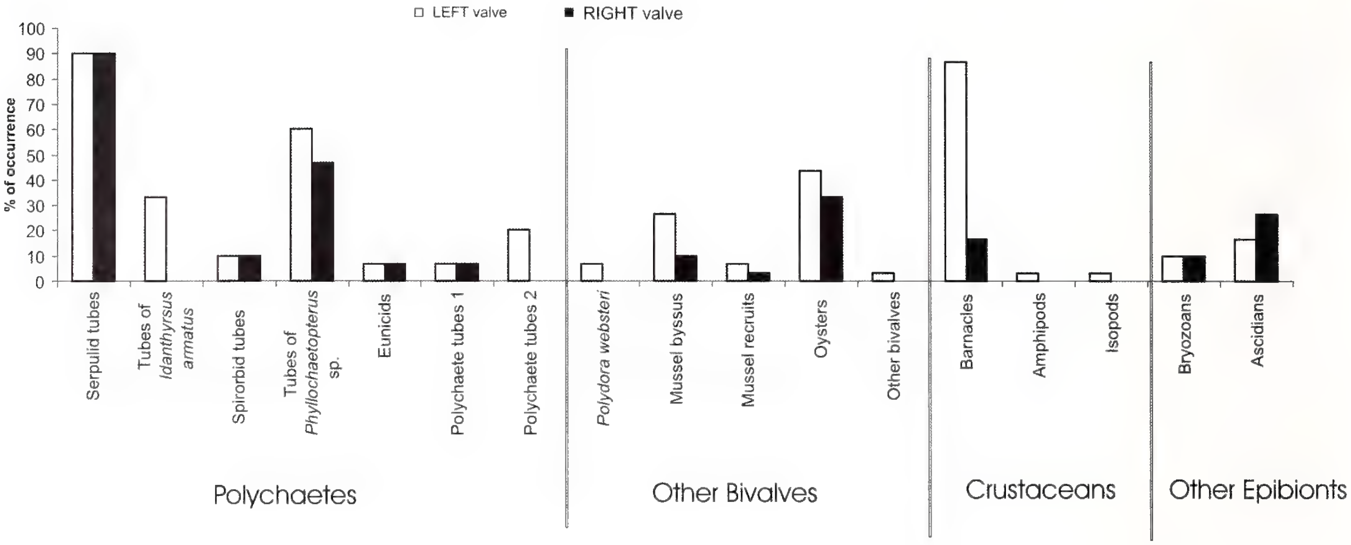

Figure 4. Frequency of occurrence of epibionts on *Flexopecten felipponei* (based on presence-absence data, N = 30).

(86.7%) left valves, but only on 5 (16.7%) of the right ones (Fig. 4). They were found most frequently on the left (upper) valves, with high values of coverage especially at regions 1, 2, 3, and 6 (Fig. 5C-D). The left valves had between 1 and 36 individual barnacles, and the right valves between 1 and 4 individuals. Region 1 of the valve was conspicuously preferred as a settlement surface; in some cases it was completely covered by barnacles (Fig. 3C).

Oysters (*Ostrea puelchana*) were found on 43.3% and 33.3% of the left and right valves, respectively (Fig. 4). They were found on both valves and in all regions (Fig. 5E-F). In many cases, the oysters completely covered the auricular areas or extended over the edges of the scallops (Fig. 3F). Numbers of epizoic oysters varied between 1 and 9. Serpulids and individuals of *Phyllochaetopterus* sp. also encrusted epizoic oysters (Fig. 3B, D, F). Recruits of the mussel *Mytilus edulis* d'Orbigny, 1846 and other unidentified small bivalves were recorded as epibionts on a few scallops (Fig. 4).

Solitary ascidians were found on 16.7% and 26.7% of the left and right scallop valves, respectively (Fig. 4). These organisms were observed in low numbers (1-2), on both valves, and in all regions (*i.e.*, Fig. 3B-D). Epizoic organisms such as bryozoan colonies, small isopods, and amphipods were also observed on a few scallops (Fig. 4). The crustaceans were free-living between the crevices in the association of epibionts.

There were no shells without epibionts; even small individuals had epizoic organisms on their valves.

Macrobenthic assemblage

Individuals of *Flexopecten felipponei* (between 16 and 90 mm maximum shell width) were primarily found associated with the tehuelche scallop *Aequipecten tehuelchus*, as part of the by-catch of the fishery. Other organisms of commercial importance found in the benthic community were the common mussel *Mytilus edulis*, the oyster *Ostrea puelchana*, and the mussel *Atrina seminuda* (d'Orbigny, 1846). A total of 69 invertebrate taxa were recorded from the study area (Table 1).

Infestation

Seven females (between 6.6 and 9.6 mm carapace length) and one male (3.8 mm carapace length) of the pea crab *Tumidotheres maculatus* (Say, 1818) were found inside eight different specimens of *Flexopecten felipponei.* Two left scallop valves were burrowed into by the parasitic polychaete *Polydora websteri.*

DISCUSSION

We found 18 epizoic taxa on the valves of *Flexopecten felipponei* from the sublittoral of Buenos Aires. The most frequent and abundant epibionts on *Flexopecten felipponei* were serpulids, barnacles, and oysters. Additional organisms such as the gastropods *Calliostoma* sp., *Crepidula* spp. and *Calyptraea* sp. occured as part of the fauna closely related with the epibiont association. Previously, only the presence of bryozoans and polychaetes on five specimens of this scallop was mentioned by Castellanos (1971).

The number of associated species greatly varies in different species of scallops recorded from different habitats. Eleven species were found on cultured *Euvola ziczac* (Linnaeus, 1758) and *Nodipecten nodosus* (Linnaeus, 1758) in Cariaco Gulf, Venezuela, but in Santa Catarina, Brazil, 16

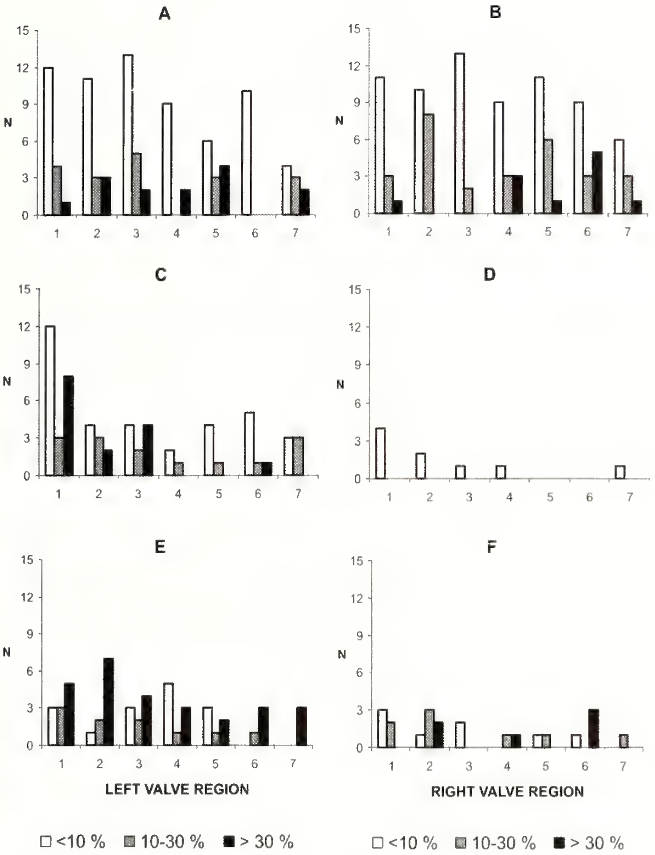

Figure 5. Portion of the surface (%) of each region of each valve of *Flexopecten felipponei* covered by: A-B, serpulids; C-D, barnacles; E-F, oysters.

species were found on *N. nodosus*. In Magdalena Bay and Bahía de la Paz, Mexico, 36 species were found inside or outside the valves of *Argopecten ventricosus* (Sowerby II, 1842) and *Nodipecten subnodosus* (Sowerby, 1835). In Tongoy, Guanaqueros, and Inglesa Bays, Chile, a total of 63 species were recorded associated with the valves of *Argopecten purpuratus* (Lamarck, 1819) (Uribe *et al.* 2001). Forty nine epizoic taxa were associated with the non-cultured species *Placopecten magellanicus* (Gmelin, 1791) in the Bay of Fundy, Canada (Fuller *et al.* 1998) and 19 sessile epizoic species were recorded on *Zygochlamys patagonica* in commercial beds of Argentina (Bremec and Lasta 2002, Bremec *et al.* 2003).

Although both valves were encrusted, the left (upper) valves had higher percentages of coverage. Except for ascidians, the epibiont species were more abundant on the left valve and occured on all regions. *Flexopecten felipponei* is a non-sedentary species that should have limited swimming capacity (Stanley 1970), which would permit it to escape from predators, as observed in other scallops (see Wilkens 1991). Epibionts can settle on both valves, depending on the living position adopted by the scallop, which seems to be more frequently with the right valve in contact with the substrate.

Surprisingly, no sponges were found on our specimens of *Flexopecten felipponei.* The symbiotic relationship between scallops and sponges has been studied worldwide (Bloom 1975, Forester 1979, Chernoff 1987, Burns and Bingham 2002, Donovan *et al.* 2002). Cover by sponges is believed to protect pectinids by camouflaging the shell and to reduce predation by asteroids by altering the surface texture of shells. Although we found sponges in the study area, they were encrusting other invertebrates, mainly crustaceans and eunicid tubes.

The majority of the epibionts on *Flexopecten felipponei* were sessile suspension-feeders. They created additional surfaces and crevices where other small free-living individuals, such as isopods and amphipods, could live. We found only a small number of free-living organisms inhabiting the epizoic association. However, we consider that the number of vagile species associated with this scallop is higher and underestimated due to the limitations of our sampling procedure.

Many of the macroinvertebrates that were part of the benthic assemblage associated with *Flexopecten felipponei* were also recorded from other middle shelf bottoms between 37°S and 39°S where the mussel *Mytilus edulis* was dominant. The coastal area of Buenos Aires is highly heterogeneous, with patches of different types of substrates, and the most diversified benthic assemblages are usually dominated by bivalves (Bremec and Roux 1997, Schejter and Bremec 2003). The settlement substrate and microhabitats provided by bivalves and associated epibionts greatly influence community structure by increasing the species richness of the benthic assemblages. In our study area, where the soft bottoms are subjected to hydrodynamic conditions that remove sediments, the scallops provided substrate for the settlement of encrusting filter feeders and permitted the colonization of coastal environments.

This is the first record of *Flexopecten felipponei* as a host of the spionid polychaete *Polydora websteri* and the pea crab *Tumidotheres maculatus.* Species of the genus *Polydora* are reported to be a pest of bivalves (Getchell 1991). They have been found in many commercial species such as *Placopecten magellanicus* (Bergman *et al.* 1982), *Argopecten purpuratus* (Basilio *et al.* 1995), *Patinopecten yessoensis* (Jay, 1857) (Mori *et al.* 1985), *Pecten maximus* (Linnaeus, 1758) (Mortensen *et al.* 2000), and *Aequipecten tehuelchus* (Ciocco 1990). Pea crabs cause slight irritation to severe structural alterations and pathology in their scallop hosts (Kruckzynski 1972, Getchell 1991, Bologna and Heck 2000, Narvarte and Saiz 2004). *Tumidotheres maculatus* was also reported inside sev-

Table 1. Invertebrates recorded from the study area.

- PORIFERA
  - Porifera unidentified
- CNIDARIA
  - *Tripalea clavaria* (Studer, 1878)
  - Actinaria unidentified
  - Hydrozoa
- ANNELIDA
  - Aphroditidae
  - *Eunice magellanica* McIntosh, 1885
  - *Chaetopterus variopedatus* (Ranier, 1807)
  - *Phyllochaetopterus* sp.
  - *Idanthyrsus armatus* Kinberg, 1867
  - *Polydora websteri* Hartman, 1943
  - Spirorbidae
  - Serpulidae
  - Maldanidae
  - Polychaeta unidentified
- MOLLUSCA
  - *Aequipecten tehuelchus* (d'Orbigny, 1846)
  - *Flexopecten felipponei* (Dall, 1922)
  - *Ostrea puelchana* d'Orbigny, 1841
  - *Pododesmus rudis* (Broderip, 1834)
  - *Mytilus edulis* d'Orbigny, 1846
  - *Atrina seminuda* (d'Orbigny, 1846)
  - *Panopea abbreviata* (Valenciennes, 1839)
  - *Pitar rostrata* (Koch, 1844)
  - Bivalve unidentified
  - *Calyptraea* sp.
  - *Crepidula* spp.
  - *Calliostoma* sp.
  - *Zidona dufresnei* (Donovan, 1823)
  - *Fissurellidea megatrema* d'Orbigny, 1841
  - Nudibranchia
  - *Octopus tehuelchus* d'Orbigny, 1834
- ARTHROPODA
  - *Peltarion spinosulum* (White, 1843)
  - *Platyxanthus patagonicus* A. Milne Edwards, 1879
  - *Coenophthalmus tridentatus* A. Milne Edwards, 1879
  - *Rochinia gracilipes* A. Milne Edwards, 1875
  - *Collodes rostratus* A. Milne Edward, 1878
  - *Pilumnoides hassleri* A. Milne Edward, 1880
  - *Leurocyclus tuberculosus* (H. Milne Edwards and Lucas, 1843)
  - *Libinia spinosa* H. Milne Edwards, 1834
  - *Pelia rotunda* A. Milne Edwards, 1875
  - *Leucipa pentagona* H. Milne Edwards, 1833
  - *Propagurus gaudichaudi* (H. Milne Edwards, 1836)
  - *Pagurus* sp.
  - Pinnotheridae
  - *Tumidotheres maculatus* (Say, 1818)
  - *Pinnixa brevipollex* Rathbun, 1896
  - *Balancus* cf. *amphitrite*
  - Lepadomorpha
  - Amphipoda unidentified
  - Isopoda unidentified

Table 1. (Continued)

- ECHINODERMATA
  - *Arbacia dufresnei* (Blainville, 1825)
  - *Pseudechinus magellanicus* (Philippi, 1857)
  - *Astropecten brasiliensis* Müller and Troschel, 1842
  - *Luidia* sp.
  - Pterasteridae
  - Asteroidea 1
  - Asteroidea 2
  - Asteroidea 3
  - Asteroidea 4
  - *Ophioplocus januarii* (Lütken, 1856)
  - *Ophiactis asperula* (Philippi, 1858)
  - *Ophiacanta vivipara* Ljungman, 1870
- BRACHIOPODA
  - *Magellania venosa* (Solander, 1816)
- BRYOZOA
  - Colonial Bryozoa unidentified
- CHORDATA
  - *Paramolgula gregaria* (Lesson, 1830)
  - *Cnemidocarpa robinsoni* Hartmeyer, 1916
  - *Pyura legumen* (Lesson, 1830)
  - *Ascidiella aspersa* (Müller, 1776)
  - *Sycozoa sigillinoides* Lesson, 1830
  - Colonial Ascidacea unidentified

eral mollusks, in the tunicate *Molgula* sp., inside tubes of the polychaete *Chaetopterus variopedatus* (Renier, 1804), and on the asteroid *Asterias vulgaris* Verril, 1866 (Fenucci 1975).

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Partulids on Tahiti: Differential persistence of a minority of endemic taxa among relict populations*

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Abstract: The extinction of many species of endemic land snails in French Polynesia because of the introduction of the carnivorous snail *Euglandina rosea* is a salutary lesson in hasty biological control undertaken without adequate scientific field trials. Fewer than 20 of the original 70+ nominal species of the family Partulidae in French Polynesia survive. In 2004 surveys were carried out in nearly 70 of the valleys of Tahiti. All of the populations found were of *Partula hyalina*, the closely related *Partula clara*, or *Samoana attenuata*. No individuals of the *Partula otaheitana/Partula affinis* complex were found, yet *P. otaheitana*, together with *Samoana burchi*, still survive in many montane forest areas (over 1000 m altitude), while *P. affinis* persists on the Peninsula of Tahiti. *Partula nodosa*, with a previous distribution of just 7 valleys, has most likely been extirpated in the wild but persists well in captive populations. The species *Partula filosa*, *Partula producta*, and *Partula cytherea* (each previously inhabiting a single valley) are almost certainly extinct, as is *Samoana jackieburchi*.

Key words: Extinctions, Partulidae, biological control, Tahiti, *Euglandina*

The endemic land snails of French Polynesia constitute a significant component of its biodiversity. Their polymorphism in shell color, banding patterns, and coiling has been the focus of classic studies in evolutionary and ecological genetics (Crampton 1916, 1932, Johnson *et al.* 1993). In the past their shells have been collected by local artisans on some islands for making shell jewelry (E. Loève, pers. comm.). The mass extinction of many of the endemic species is an example of a disastrous attempt at biological control without adequate field trials (Clarke *et al.* 1984, Cowie 1992). The giant African snail *Lissachatina fulica* (Bowdich, 1822) was introduced as a food resource in 1967, but spread rapidly and destructively. The solution at the time was wrongly perceived to be the introduction of the carnivorous snail *Euglandina rosea* (Férussac, 1821), which took place on Tahiti in 1974, on Moorea in 1977, and on other islands in the 1980s and 1990s. The predators preferentially attacked the smaller endemic species, notably members of the family Partulidae. Over half of the 120 known species of the family Partulidae were native to French Polynesia. Sadly now most are extinct (Murray *et al.* 1988).

An international captive breeding effort—the only one in the world for an invertebrate family—has continued to maintain a number of species of *Partula* that no longer exist in the wild (Pearce-Kelly *et al.* 1997). An *ad hoc* program of field surveys has been carried out in the Society Islands of French Polynesia over the last few years to establish the exact status of remaining species in their natural habitat and to locate any relict populations that may have survived the ravages of the last 20 years. These surveys have concluded that there is a high probability of virtually all species being extinct on the islands of Bora Bora, Huahine, Raiatea, and Tahaa, and that only Moorea and Tahiti still support remnant populations (Coote and Loève 2003), though there have been recent discoveries of a few partulid individuals on the highest peaks of Huahine and Raiatea (J.-Y. Meyer, pers. comm.). This paper concentrates on a major effort to survey Tahiti Nui, which comprises the bulk of the island of Tahiti—the peninsula of Tahiti Iti has yet to be surveyed.

Tahiti is by far the largest island in French Polynesia. The American biologist, H. E. Crampton (1916) made an extensive study-collection of the genus *Partula* from over 60 valleys (50 on Tahiti Nui and 12 on Tahiti Iti) between 1906 and 1909. The malacologists Y. Kondo and J. B. Burch collected from 33 valleys in 1970 (Anonymous 2004). With the introductions of *Euglandina rosea* to Tahiti in 1974, the first such introduction in French Polynesia, focus changed from pure research to conservation. While undertaking large-scale surveys and emergency collections on Moorea, Murray *et al.* (1988) also undertook smaller surveys of valleys on Tahiti. They searched 11 valleys on visits between 1980 and 1987. Extrapolating from the situation on Moorea, they believed that all species from Tahiti would be extinct within a few years, as many of the valleys were found to be empty already. However, in 1995 a visiting team of biologists from the U.K. and U.S.A., acting on local advice, found thriving populations on Mt. Marau and in the valleys of Te Pari ("the cliffs") on Tahiti Iti. Since that year, a number of isolated populations have been discovered at different locations on Tahiti, some of which have since disappeared (Coote *et al.* 1999).

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METHODS

Although the nature of the habitat and terrain would have changed almost beyond recognition since his time, the information in Crampton (1916) has still formed the basis of the surveys reported here. Details were refined on the ground, with 1:20,000 scale maps and advice from local people. The majority of the surveys took place between January and September 2004, in the hotter rainy season and the cooler drier season. Each survey of a valley was restricted to a single day. Because of the extreme rarity (and possible non-existence) of partulids in the valleys, simple searches for their presence or absence were carried out in habitats that experience suggested were most amenable to their survival and which were accessible. Using existing forest trails where available and continuing as deep as possible into the valleys, the areas searched were usually patches of around 5 m^2 in size. Where populations were found, all snails seen within the immediate patch were counted inside 20 minutes and descriptive details recorded. Dead shells were collected; those of *Euglandina rosea*, being large and conspicuous, were easily seen.

RESULTS

Seventy-six valleys on Tahiti Nui were identified and 69 of them were surveyed (including 22 on two or more occasions). Access could not be gained to the other 7 valleys. Live populations of partulids were found in 22 valleys (Table 1).

There was no obvious geographical pattern to these finds. They occurred in the north, east, west, and south, in

Table 1. Valleys on Tahiti Nui where partulids survive.

Valley	Administrative commune	Species found	No. of populations	Individuals counted in 20 minute search	Valley type
Fautaua-Faaiti	Papeete	*Partula hyalina*	1	10	Small, dry
Pirae	Arue	*Partula hyalina*	1	*	Large, dry
Ahonu	Mahina	*Partula hyalina*	1	5	Medium, wet
Puhi	Hitia'a O Te Ra, Papenoo	*Partula clara*	1	2	Small, wet
Faarapa	Hitia'a O Te Ra, Papenoo	*Partula hyalina, Partula clara*	Several	5 (hy) 3 (hy) 4 (cl)	Small, wet
Vaipu (Faaromai)	Hitia'a O Te Ra, Tiarei	*Partula hyalina*	1	2	Small, wet
Haapoponi	Hitia'a O Te Ra, Tiarei	*Partula hyalina, Partula clara, Samoana attenuata*	Several	9 (hy) 5 (hy) 3 (cl) 8 (hy) 5 (hy) 4 (cl)	Small, wet
Onohea-Faaiti	Hitia'a O Te Ra, Tiarei	*Partula hyalina, Partula clara*	2	12 (hy) 17 (cl)	Small, wet
Tahaute	Hitia'a O Te Ra, Mahaena	*Partula hyalina*	1	2	Large, wet
Faaiti	Hitia'a O Te Ra Hitia'a	*Partula hyalina*	1	2	Small, wet
Vaiiha (Papeiha)	Hitia'a O Te Ra, Hitia'a	*Partula hyalina, Partula clara*[1]	1	11 (hy) 2 (cl)	Large, wet
Vaitoare	Taiarapu Est, Faaone	*Partula hyalina, Partula clara*	Several	1 (hy) 5 (hy) 1 (cl) 18 (hy) 2 (cl)	Small, wet
Apirimaue*	Teva-I-Uta, Papeari	*Samoana attenuata*	1	—	Large, wet
Vaioo	Teva-I-Uta, Mataiea	*Partula clara*	2	2 6	Small, wet
Faurahi*	Teva-I-Uta, Mataiea	*Partula clara*[1]	1	—	Medium, wet
Taapua	Papara	*Partula clara*	1	1	Medium, wet
Tereia*	Papara	*Samoana attenuata*	1	—	Medium, wet
Tiapa (Hopuetama)	Paea	*Partula clara, Samoana attenuata*	1	14 (hy) 1 (at)	Medium, dry
Papehue	Paea	*Partula clara, Samoana attenuata*	1	1 (cl) 1 (at)	Medium, dry
Maruapo	Punaauia	*Partula clara*	1	4	Small, dry
Matatia	Punaauia	*Partula hyalina*	1	3	Small, dry
Tipaerui	Faa'a	*Samoana attenuata*	1	1	Medium, dry

* Population found by W. Teamotuaitau.

[1] Live *Euglandina rosea* found in valley.

hy = *Partula hyalina;* cl = *Partula clara;* at = *Samoana attenuata.*

valleys big and small, dry and wet (Table 1), although there was a slight tendency for there to be more living snails in the small, wet valleys of the east coast. On the other hand, there was a striking pattern in the persisting species. Apart from a few individuals of the rare *Samoana attenuata* (Pease, 1864), the only snails discovered were of *Partula hyalina* (Broderip, 1832) and the very similar *Partula clara* (Pease, 1864) (Fig. 1). Nearly 76% of the populations of *P. hyalina* and 40 % of *P. clara* were found on one native plant species, the wild red ginger *Etlingera cevuga* (opuhi maohi).

Live individuals of the carnivore *Euglandina rosea* were found in just 10 valleys, including 3 adjacent valleys in Papeari. It does not appear to be an immediate threat to any of the surviving valley populations of partulids on Tahiti Nui. In no valley did I find more than one individual of *E. rosea*.

In addition to the valleys, five mountain tracks on Tahiti Nui and one above Taravao Plateau on Tahiti Iti were surveyed. The conditions for snails are very different above 1000 m elevation compared to the lowland areas of disturbed habitat (Fosberg 1992). In contrast to the valleys, the dominant partulid species surviving in montane forests is *Partula otaheitana* (Bruguière, 1792).

The largest populations still survive above 1000 m on Mt. Marau. These consist principally of different forms of *Partula otaheitana*, but also *Samoana burchi* (Kondo, 1973), a species believed extinct (Murray *et al.* 1988) but recently confirmed by molecular analysis (T. Lee, pers. comm.). Several populations of more than 30 individuals still survive in patches along the trail to Mt. Aorai, although individuals of *Euglandina rosea* are often seen at around 800 m altitude and also at 1200 m encroaching into partulid populations. No live partulids were found on the route to Mt. Mauru (where they were last seen in 2002) or from the Sentier de Milles Source to the summit of Mt. Pihaiateta (600 m to 1400 m), although they have since been seen on the latter trail (B. S. Holland, pers. comm.). In neither place did it appear that the populations had fallen victim to *E. rosea*. In contrast, along the trail from Pic Rouge to Masif du Pic Vert, there were live individuals of *E. rosea* and many empty shells of partulids. Above Plateau Taravao on Tahiti Iti, populations of partulids persist, even though *E. rosea* is also present.

DISCUSSION

The discovery in 1995 of apparently thriving populations of species of partulids previously believed extinct was a surprise (Murray *et al.* 1988). This led to a renewed search for endemic snails in 2001. Most of these searches took place at high altitudes (over 1000 m) where surveys and information from local biologists and mountain guides confirmed the presence of small isolated populations on the mountains Mauru, Tahiti, Aorai, and Atara and on the plateaus Faufiru and Terepo. The presence of the majority of endemic plant species at high altitude meant that these areas are regularly visited by botanists and good information was available. Because shells of *Euglandina rosea* but no live animals had been found among the partulid populations of Mt. Marau, it appeared that the predatory snail had reached the area but had not thrived there. This led to the suggestion that an altitudinal ceiling may exist for the principal agent involved in the extinction of Society Island partulids (Gerlach 1994). This did not, however, explain the abundant partulid populations remaining at sea level in the Te Pari district of Taiarapu Peninsula (Tahiti Iti). Whereas in 1995 there had been no evidence of the predator in this small arc of valleys in the extreme southeast, in the following years *E. rosea* spread quickly until by 2001 it had reached every valley.

An upgrade in the existing level of protective legislation has been proposed in order to safeguard the populations of partulids surviving above 1000 m altitude (Meyer *et al.* 2005) because the terrain would not be amenable to physical protection in the form of predator-proof protected area, a method being tested at lower elevations (Coote *et al.* 2004). However, if there were any surviving populations threatened by *Euglandina rosea* at low altitudes in the valleys of Tahiti, then measures such as reserves could be considered as realistic options. Because of the size and topographical nature of Tahiti, a systematic search of the valleys required a long time and extensive planning. Until the resources became available in 2003, these barely seemed to be viable options. Given the timescale of the contract, valleys on Tahiti Iti were unable to be included in the surveys.

It became clear after the first few discoveries of valley populations that only three species persisted and that all the others had most likely been extirpated. By far the most common species were the universally white *Partula hyalina* and the very similar *Partula clara*, which is polymorphic in shell color. The third species, *Samoana attenuata*, has a distribution and ecology that differs from most of the species in the genus *Partula*. It has always been a rare species, made elusive by the fact that it favors higher branches in the trees (Crampton 1916). It has also survived on the neighboring island of Moorea (Coote 1999). In the lowland forests of Tahiti it was represented in the current surveys by just a few individuals that were found occasionally.

No individuals of *Partula otaheitana* or *Partula affinis* (Pease, 1867) were found in any of the valleys of Tahiti Nui, yet in Crampton's 1906-09 collections *P. otaheitana* (of which at the time *P. affinis* was considered a subspecies) formed over 90% of all valley collections, except in the 7 valleys that had *Partula nodosa* (Pfeiffer, 1851) (Crampton 1916). *Partula nodosa* is now considered as extinct in the wild, although it persists well in captivity (P. Pearce-Kelly, pers. comm.). In contrast, *Partula hyalina* and *Partula clara* together accounted for just over 5% of those same collections. Ratios of species similar to those reported by Crampton were found by researchers up until the introduction of *Euglandina rosea* in 1974 (J. B. Burch, pers. comm.). Emerging molecular evidence suggests that *P. hyalina* and *P. clara* should be synonymized (D. Ó Foighil, pers. comm.).

Tahiti Nui is divided ecologically into those valleys on the dry leeward side of the island, roughly between Mahina in the north and Pointe Maraa in the southwest, and the wet valleys that constitute the remainder. The flora is quite different in the two regions. Most noticeable is the distribution of the dominant alien plant pest species, *Miconia calvescens*, abundant in the eastern valleys but rarer in the drier western ones. In terms of partulid distribution, Crampton (1916) maintained that *Partula hyalina* occurred across the whole island, but preferred drier areas, and *Partula clara* was absent from the driest quadrant. However, there appeared little preference for any type of valley for either species, both being found in dry and wet, large and small. The densest and most widespread populations of both these species were, however, found in the small, wet valleys of the northeast.

Not enough is known about the ecology of the surviving species to determine why they should have escaped to some degree the ravages of *Euglandina rosea*, which has left extinct so many others across the Society Islands (Clarke *et al.* 1984, Murray *et al.* 1988, Cowie 1992). *Partula hyalina*, however, differs from the other species on Tahiti in that it is the only French Polynesian species of *Partula* that was not a single island endemic, occurring also on four of the Austral Islands and three of the Cook Islands (Crampton 1916). Because of this distribution, it was believed to be an ancient species (Crampton 1916), especially because it was universally white, in contrast to the conspicuous polymorphism of many other partulids in the Society Islands (Crampton 1916, 1932). However, recent genetic analysis confirms that some individuals of *P. hyalina* from the Austral Islands share mitochondrial haplotypes with those on Tahiti, suggesting evolutionarily recent among-archipelago dispersal (D. Ó Foighil, pers. comm.). *Partula hyalina* was generally the first species to be seen on entering valleys—in other words, it more easily tolerated disturbed (and drier) habitats (Crampton 1916). The finds during the current surveys confirm this ecological distribution.

As a result of these surveys the distribution of the remaining partulid species on Tahiti Nui can best be summarized thus: below 250 m altitude, *Partula hyalina*, *Partula clara*, and *Samoana attenuata*; between 250 m and 1000 m, none; above 1000 m, *Partula otaheitana* and *Samoana burchi*. *Partula affinis* seems to have disappeared from Tahiti Nui, but still survives on Tahiti Iti. *Partula nodosa* has been extirpated from the wild but is maintained in captivity. The two single-valley endemics, *Partula filosa* (Pfeiffer, 1851) and *Partula producta* (Pease, 1864), as well as two rare species of unclarified taxonomy, *Partula cytherea* (Crampton and Cooke, 1930) and *Samoana jackieburchi* (Kondo, 1981) are almost certainly extinct. The surviving populations of partulids in the valleys of Tahiti do not appear to be under any immediate threat apart from that of external forces acting on small population size, generally less than 50 individuals. A number of colonies are being regularly monitored for changes in their populations or their habitats.

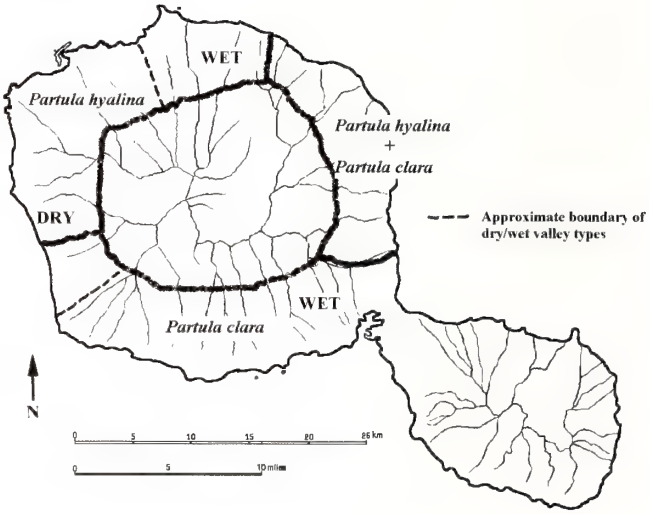

Figure 1. Current distributions of *Partula hyalina* and *Partula clara* on Tahiti.

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Phyllidiidae (Opisthobranchia: Nudibranchia) from Papua New Guinea with the description of a new species of *Phyllidiella*

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Abstract: Species of phyllidiid nudibranchs from Papua New Guinea (and other Indo-Pacific regions) are redescribed in this paper. A new species, *Phyllidiella backeljaui* n. sp., is described and compared with other species of the genus. External characters and internal morphology of the species studied have been examined in detail and illustrated, some of them for the first time such as *Phyllidiopsis pipeki*. In addition, new locations for *Phyllidiella hageni* and *Phyllidiella zeylanica* are reported from Papua New Guinea.

Key words: phyllidiid, morphology, anatomy, new species, new locations

The family Phyllidiidae Rafinesque, 1814 includes gastropods belonging to the order Nudibranchia (Gastropoda: Opisthobranchia). It is widely distributed throughout the tropical Indo-West Pacific Ocean (Risbec 1928, 1956, Baba 1930, Edmunds 1971, 1972, Baba and Hamatani 1975, Lin 1983, Willan and Coleman 1984, Willan *et al.* 1998, Fahrner and Beck 2000). They are predators specializing in suctorial feeding on sponges and have developed a highly toxic chemical defense. This family is characterized by the absence of a dorsal gill, the possession of secondary gill leaflets that are located ventrally around the foot, and by the absence of radula and jaws (Bergh 1869, 1875, Pruvot-Fol 1956, 1957, Brunckhorst 1990a, 1993, Willan *et al.* 1998, Fahrner and Beck 2000).

Several authors have paid special attention to this complicated group, but there is still a great deal of confusion about the correct identification of these specimens, which have been the subject of numerous disagreements (Wägele 1985, Yonow 1986, Brunckhorst and Willan 1989, Gosliner and Behrens 1988, Brunckhorst 1989, 1993, Fahrner and Beck 2000). The main reasons for the misidentifications are the large number of descriptions based on single preserved specimens, the restriction on features of external morphology, and intraspecific variability. Only a few authors have recognized the necessity of accurate anatomical examination for the description of new species (Pruvot-Fol 1956, 1957, Gosliner and Behrens 1988, Brunckhorst 1989, 1990a, 1990b, 1993, Yonow 1996, Fahrner and Beck 2000).

The phyllidiid fauna of the Indo-Pacific was comprehensively reviewed by Brunckhorst (1993), although anatomical data could not be provided for all of the species. Only the type species of each genus was studied anatomically.

Ghiselin (1992) compiled a faunal list from Madang Province, Papua New Guinea. The list represents collections made in Madang by T. Gosliner and M. Ghiselin in 1986 and 1989, T. Gosliner and R. Willan in 1988, T. Gosliner and G. Williams in 1990, and T. Gosliner, G. Williams, and M. Ghiselin in 1992. He concluded that the opisthobranch fauna of the Madang Province is very rich in species and still poorly known. The family Phyllidiidae is particularly conspicuous and abundant.

The present paper is a contribution to the knowledge of phyllidiid fauna based on studies of specimens collected from Papua New Guinea. A few animals from other regions of the Indo-Pacific Ocean are also included. All the species studied are described and illustrated, some of them for the first time. New records for some species are reported from Papua New Guinea, including the very uncommon species *Phyllidiella hageni* Fahner and Beck, 2000, only known to date from Lombok, Indonesia, and *Phyllidiella zeylanica* (Kelaart, 1858), which is moderately common in the Indian Ocean but rare in the western Pacific (Fahrner and Beck 2000). A description of a new phyllidiid species, *Phyllidiella backeljaui* n. sp., is also included in this paper.

MATERIAL AND METHODS

A total of 150 specimens belonging to 13 species of phyllidiid nudibranchs were studied. Seventy specimens were collected during July and August 1996 by J. S. Troncoso and deposited at the Department of Ecology and Animal Biology of the University of Vigo (Spain). The holotype and paratype of the new species, *Phyllidiella backeljaui*, was deposited at the Museo Nacional de Ciencias Naturales of Madrid. The remaining specimens were borrowed from the Royal Belgian Institute of Natural Sciences for identification and are denoted by the abbreviation RBINS.

Most of the studied specimens were collected on the northern coast of Papua New Guinea (PNG) in 1996, mainly in the low coral formation of Laing Island, which is located in Hansa Bay (Domínguez *et al.* 2004). Some specimens were collected at other sites in the bay, including Durangit Reef and Boisa Island. A few animals of the Royal Belgian Institute of Natural Sciences collection were collected from Nossi-Bé (Madagascar), and Îlot Tabou (New Caledonia).

We do not have information about how the specimens deposited at the RBINS were collected and preserved. The specimens captured in 1996 were collected subtidally using SCUBA and intertidally in shallow water. In the laboratory, photographs of live specimens were taken of most of the species before they were anesthetized. The animals were frozen at 0°C prior to fixation in 5% formalin in seawater for 24-48 hours, then transferred to 70% ethanol.

Preserved specimens were measured and examined in detail. All specimen dimensions are given as body length x maximum body width. The drawings of external morphology are based on preserved specimens. All animals were dissected by a dorsal longitudinal incision while viewed with a binocular dissecting microscope. For the illustrations of internal anatomy, the blood gland, aorta, and reproductive system were removed from their natural positions.

SPECIES DESCRIPTIONS

Phyllidia varicosa Lamarck, 1801
(Figs. 1A, 2)

Phyllidia varicosa Lamarck 1801: 66, Edmunds 1971: 388-389, fig. 23, Baba and Hamatani 1975: 174-175, fig. I, Brunckhorst 1993: 26-29, figs. 2, 3A, 23, 24A-D, pl. 1A-D, Debelius 1996: 123, 241, 265, Fahrner and Beck 2000: 202, pl. 2, fig. 6, Fahrner and Schrödl 2000: 164-171, Yonow *et al.* 2002: 863.

Phyllidia trilineata Cuvier 1804: 268, pl. A, figs. 1-6.

Phyllidia arabica Ehrenberg 1831: pages unnumbered.

Material examined

RBINS: Nossi-Bé (55.7 mm × 30.1 mm); PNG (38.6 mm × 14.5 mm, 48.3 mm × 13.5 mm, 54.3 mm × 22.0 mm, 37.5 mm × 11.2 mm, 36.6 mm × 16.8 mm, 41.9 mm × 18.5 mm, 25.2 mm × 9.1 mm, 31.5 mm × 11.4 mm, 43.3 mm × 17.0 mm, 42.1 mm × 19.1 mm, 46.9 mm × 17.5 mm, 60.2 mm × 25.1 mm, 36.6 mm × 14.8 mm, 53.1 mm × 29.3 mm, 43.5 mm × 18.6 mm, 56.0 mm × 19.8 mm); Laing Island (28.8 mm × 17.2 mm, 65.0 mm × 35.7 mm, 30.8 mm × 15.0 mm, 35.4 mm × 18.8 mm).

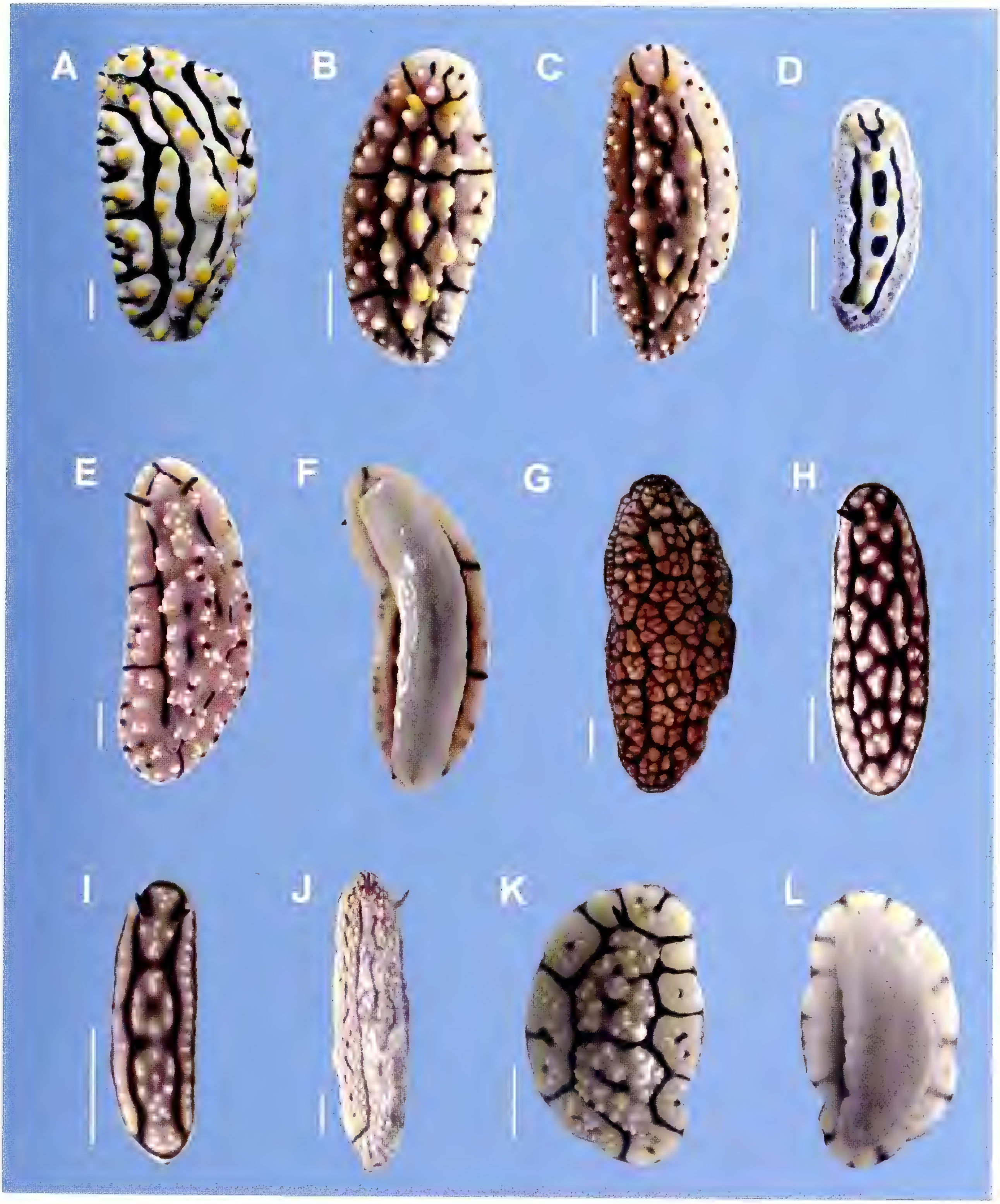
Expedition 1996: Laing Island, 0.5 m depth (49.6 mm × 30.4 mm, 50.9 mm × 26.5 mm, 46.7 mm × 26.55 mm, 28.7 mm × 16.3 mm, 17.6 mm × 9.0 mm, 14.2 mm × 7.6 mm, 40.0 mm × 16.3 mm, 48.7 mm × 26.1 mm); Laing Island, 15 m depth (30.5 mm × 15.2 mm); Laing Island, 16.5 m depth (32.1 mm × 16.0 mm, 50.9 mm × 26.3 mm); Laing Island, 18.5 m depth (33.2 mm × 17.4 mm, 43.0 mm × 24.3 mm, 40.9 mm × 21.3 mm, 43.2 mm × 18.0 mm); Hansa Bay, 28.8 m depth (25.0 mm × 12.9 mm).

Description

All of the specimens share the presence of three longitudinal ridges of tubercles on the median region of the dorsum, separated from each other and from the lateral pustules by bands of dark pigmentation. Many animals have broken ridges and the dorsal bands are interconnected; some specimens have continuous ridges and isolated bands (Fig. 2A). On the sides of the dorsum there are rounded or conical tubercles that form transverse ridges. The live animals (Fig. 1A) have yellow rhinophores and the tubercles are blue-grey at their bases and have yellow-orange apices. Some preserved specimens lack the dorsal black pigmentation. Ventrally the pedal sole has a median black longitudinal stripe that is well preserved in some specimens and partially absent in others.

Internally (Fig. 2B), the short oral tube sometimes has black marks on its sides; the pharyngeal bulb is wide and there are rounded oral glands on either side of it. The pharyngeal retractor muscles are well developed and short and are inserted dorsally onto the pharyngeal bulb. The tubular pharynx leaves the bulb dorsally. The esophagus inserts into the digestive gland mass; the intestine originates to the left of the pericardium, turns to the right and extends to the anal papilla. The reproductive system (Fig. 2C) has a spherical ampulla whose color is pale orange or brown in the preserved state. It connects with a thick and convoluted prostate, which narrows into a short vas deferens. The nidamental gland mass is large and spherical. The bursa copulatrix is spherical and lies next to the receptaculum seminis, which is kidney-shaped. The vaginal duct is long and slightly folded.

Figure 1. Photographs of live specimens used in this study. The orientation is anterior at top in all. A, *Phyllidia varicosa*, dorsal view (Laing Island, depth 18.5 m). B-C, *Phyllidia elegans*, dorsal view (Laing Island, depth 17.4 m). D, *Phyllidia coelestis*, juvenile in dorsal view (Laing Island, depth 17.4 m). E, *Phyllidiopsis krempfi*, dorsal view (Boisa Island, depth 56.4 m). F, *Phyllidiopsis krempfi*, ventral view. G, *Phyllidiella pustulosa*, dorsal view of a large specimen (Laing Island, depth 0.5 m). H, *Phyllidiella pustulosa*, dorsal view of a smaller specimen. I, *Phyllidiella pustulosa*, juvenile in dorsal view. J, *Phyllidiella hageni*, dorsal view (Laing Island, depth 16.5 m). K, *Phyllidiella backeljaui* n. sp., dorsal view (Laing Island, depth 9 m). L, *Phyllidiella backeljaui* n. sp., ventral view. Scale bars = 5 mm.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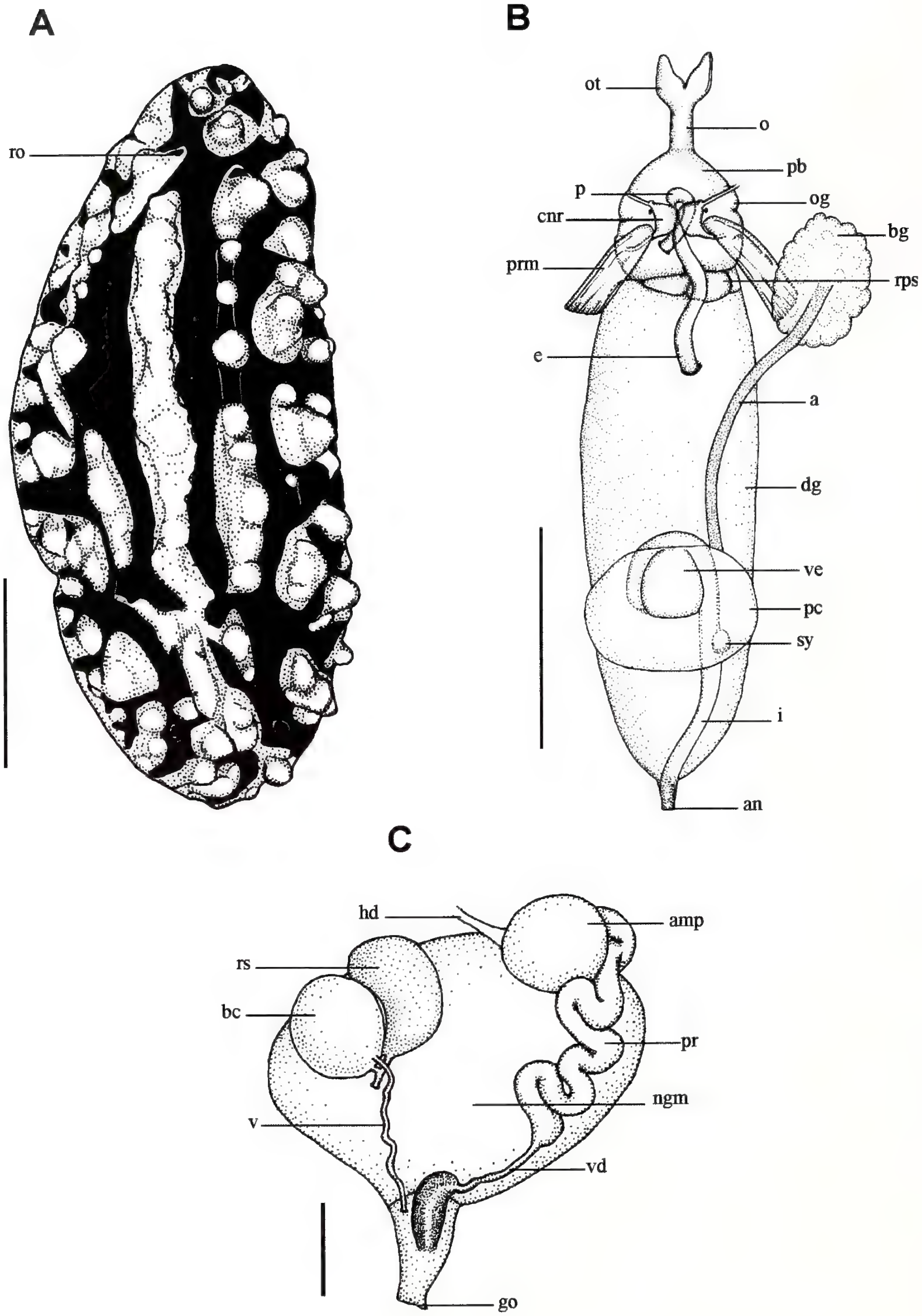
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Remarks

The taxonomic status of *Phyllidia varicosa* Lamarck, 1801 has been the subject of considerable debate for several years (Fahrner and Schrödl 2000). The reason for this controversy was the description of a specimen, on the basis of which Cuvier (1797) established the genus *Phyllidia* and which was considered lost since 1866 (Willan *et al.* 1998). These authors rediscovered the holotype in Paris, which was in a good state of preservation. The holotype has weak, dark marks forming a longitudinal line on the sole; however, this characteristic is not always present in the preserved state. Some specimens appear to have completely lost the black pigmentation dorsally and ventrally, including the stripe on the foot.

Phyllidia elegans Bergh, 1869
(Figs. 1B-C, 3)

Phyllidia elegans Bergh 1869: 439-454, 506-507, pl. 18B, 19, Allan 1957: 5, Coleman 1989: 48, Brunckhorst 1993: 33-34, fig. 25C, pl. 2A-B, Wells and Bryce 1993: 146, species number 190, Debelius 1996: 264, Gosliner *et al.* 1996: 168, species number 594, Marshall and Willan 1999: 122, fig. 220, Fahrner and Beck 2000: 202, pl. 2, figs. 7-8.

Material examined

RBINS: Laing Island (45.2 mm × 18.7 mm).

Expedition 1996: Laing Island, 14.1 m depth (14.1 mm × 6.0 mm), 17.4 m depth (23.8 mm × 12.8 mm, 26.7 mm × 13.0 mm).

Description

Dorsally and medially, there are three longitudinal rows of tubercles that can be simple and rounded, irregular, or coalesced, but never form ridges. The central row ends at the anal opening; the other two begin behind each rhinophore. We observed the coloration in life of two specimens (Figs. 1B, C): the tubercles are creamy-pink with whitish apices. Some tubercles of the median part of the dorsum have yellow apices. The rhinophores are yellow. There are two longitudinal black lines that surround the central area of the dorsum including the rhinophores and the anus; they are joined in some specimens by a black transverse band. The central row of tubercles are sometimes separated from the other ones by a longitudinal black line to each side, or its tubercles may be separated from each other by short, irregular lines. On the mantle margin there are transverse black lines that extend to the mantle edge. Ventrally the sole has a longitudinal black line and there are also black lines on the sides, next to the gills (Fig. 3A). These lines appear to be a bit faded, as in the largest specimen, but they are visible in all specimens.

Internally (Fig. 3B), the short oral tube has a transverse black band at its base. The pharyngeal retractor muscles insert dorsally onto the thick pharyngeal bulb, which is covered with oral glands. The pharynx arises posteriorly from the pharyngeal bulb, extends in front and passes through the central nerve ring. The esophagus inserts into the digestive gland mass. The intestine originates to the left of the pericardium, turns to the right and extends to the anal papilla, which is swollen. The reproductive system (Fig. 3C) has a large, spherical, yellow ampulla. The prostate is folded near the ampulla and it narrows into a short vas deferens. The bursa copulatrix and the receptaculum seminis are small and connected by a short duct that inserts in the female gland. The vaginal duct is very narrow and slightly folded.

Remarks

The pattern of black lines varies intraspecifically; the tubercles do not form continuous ridges, although they may have their bases fused together. *Phyllidia elegans* displays some ontogenetic and individual variations in the arrangement of notal tubercles (Brunckhorst 1993) and some specimens may have only one or just a few yellow capped pustules (Marshall and Willan 1999). However, the coloration and the black markings serve to distinguish it from other related species (Brunckhorst 1993). These features are the pink dorsum with tubercles capped in yellow, black marks on dorsum, and the black line on the foot sole and on its sides.

Phyllidia coelestis Bergh, 1905
(Figs. 1D, 4)

Phyllidia coelestis Bergh 1905: 182-183, pl. 3, fig. 16, Coleman 1989: 49, Brunckhorst 1989: 35-45, figs. 1-4, Brunckhorst 1993: 30-33, fig. 25B, pl. 1F-H, Allen and Steene 1994: 200, Gosliner *et al.* 1996: 168, species number 593, Debelius 1996: 264, Marshall and Willan 1999: 121-122, fig. 219, Fahrner and Beck 2000: 202, pl. 3, fig. 1, Yonow *et al.* 2002: 862, fig. 16B.

Figure 2. *Phyllidia varicosa.* A, Drawing of the dorsal surface of a preserved specimen 40.0 mm long collected in Laing Island, depth 0.5 m. B, Diagram of the internal anatomy. C, Diagram of the dorsal view of the reproductive system. Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; go, genital opening; hd, hermaphrodite duct; i, intestine; ngm, nidamental gland mass; o, oral tube; og, oral gland; ot, oral tentacles; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; prm, pharyngeal retractor muscle; ro, rhinophoral opening; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 10 mm (A, B), 1 mm (C).

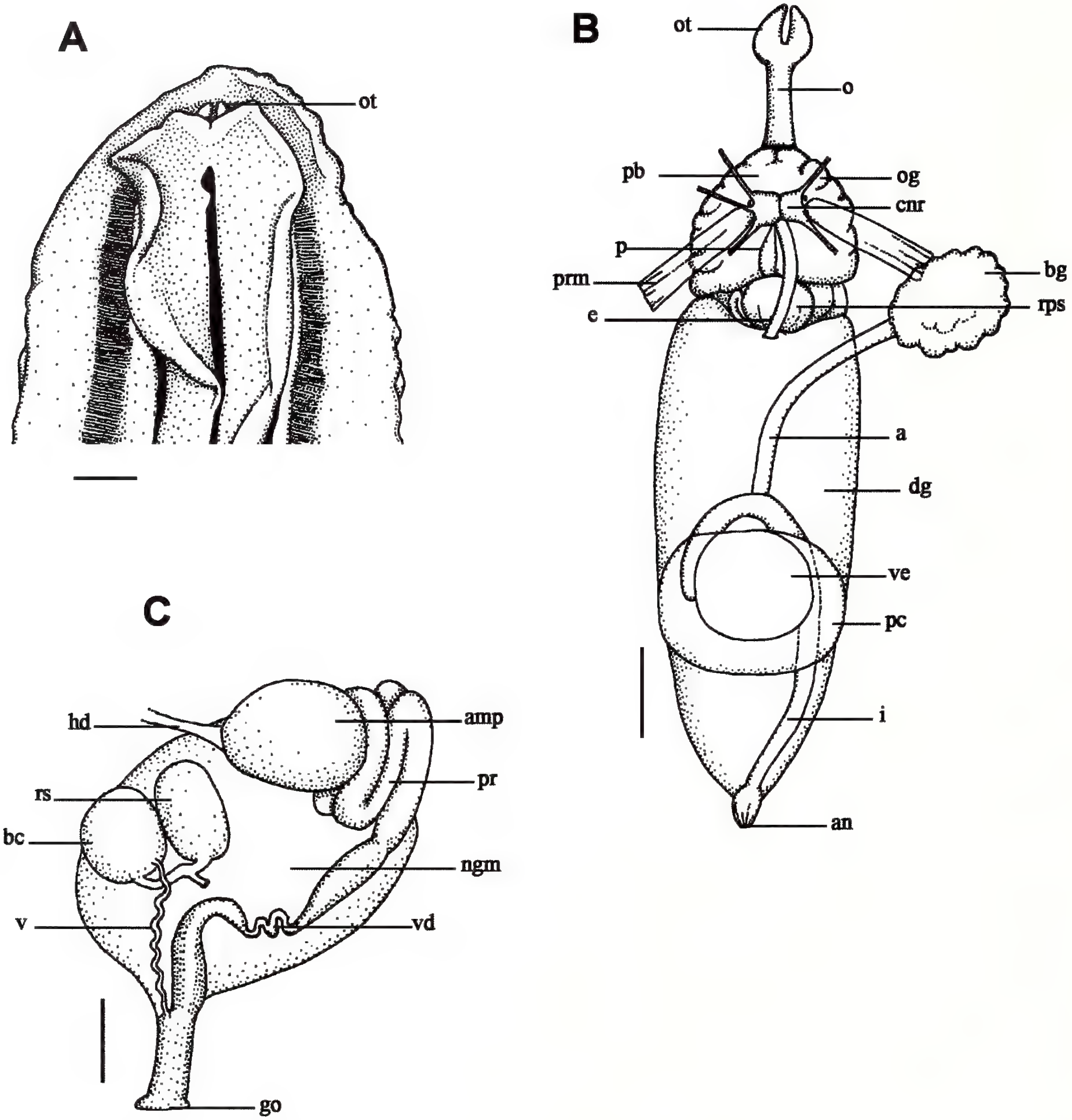

Figure 3. *Phyllidia elegans*. A, Drawing of the anterior end of the ventral surface of a preserved specimen 23.8 mm long, collected in Laing Island, depth 17.4 m. B, Diagram of the internal anatomy. C, Diagram of the dorsal view of the reproductive system (the same specimen illustrated in Fig. 3A). Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; go, genital opening; hd, hermaphrodite duct; i, intestine; ngm, nidamental gland mass; o, oral tube; og, oral gland; ot, oral tentacles; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; prm, pharyngeal retractor muscle; rps, reproductive system; rs, receptaculum seminis; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 2 mm (A, B), 1mm (C).

Phyllidia alia Yonow 1984: 224, figs. 6C-D, 7A, 8F-G.
Phyllidia varicosa Gosliner 1987: 90, pl. 152 (non *Phyllidia varicosa* Lamarck, 1801).

Material examined

RBINS: PNG (28.7 mm × 12.4 mm, 20.3 mm × 12.0 mm, 23.3 mm × 11.5 mm, 30.9 mm × 12.7 mm, 24.4 mm × 10.6 mm, 27.9 mm × 14.1 mm); Laing Island (14.1 mm × 8.8 mm, 27.9 mm × 12.2 mm, 18.8 mm × 11.0 mm, 18.3 mm × 9.5 mm, 18.8 mm × 9.7 mm, 22.2 mm × 9.7 mm, 19.2 mm × 9.0 mm, 20.1 mm × 9.8 mm).

Expedition 1996: Laing Island, 0.5 m depth (19.2 mm × 9.8 mm, 10.2 mm × 4.8 mm), 14.1 m depth (30.0 mm × 14.4 mm, 12.4 mm × 6.1 mm), 14.7 m depth (11.5 mm × 4.9 mm), 15 m depth (23.6 mm × 9.4 mm), 15.7 m depth (15.0 mm × 8.2 mm), 16.5 m depth (17.7 mm × 10.1 mm), 17.4 m depth (20.0 mm × 8.3 mm, 14.6 mm × 8.5 mm), 17.8 m depth (14.5 mm × 6.3 mm), 45 m depth (17.9 mm × 8.0 mm).

Description

Living specimens of *Phyllidia coelestis* have blue dorsal surfaces with black bands and rounded tubercles capped in yellow that form three longitudinal rows. The median row is formed by single isolated tubercles, separated from each other by black patches. This row begins anterior to the yellow rhinophores and its posterior tubercles are smaller and may be coalesced. The anal opening is located at the posterior end of this row. The other two rows begin directly behind each rhinophore with a high, rounded, and isolated tubercle. They continue with a series of tubercles forming a ridge. These are followed by two wide black bands with wavy external borders. The mantle margin is broad with rounded tubercles and small black spots, which may be lacking in smaller specimens. In juvenile specimens (Fig. 1D), there is a black "Y" on the anterior part of the dorsum between the rhinophores. Ventrally (Fig. 4A), the foot sole has no black marks and the oral tentacles are separate.

Internally (Fig. 4B), the oral tube has black marks next to the oral tentacles and a transverse black band at its base. On the pharyngeal bulb there are spherical oral glands and the pharyngeal retractor muscles insert dorsally onto the bulb. The pharynx passes through the central nerve ring and connects with a narrow esophagus that inserts into the digestive gland mass. The reproductive system (Fig. 4C) has a large ampulla and the prostate connects to a narrow vas deferens. The largest specimens (41 mm long) possess seminal receptacle longer than the bursa copulatrix. In smaller specimens both organs are the same shape and size. The vaginal duct arises from the bursa copulatrix and is very narrow.

Remarks

Specimens of *Phylidia coelestis* can be distinguished from those of other species by the presence of three rows of tubercles on the median part of the dorsum that are isolated in the midline and two other rows forming ridges (the ridges can be interrupted). The living animals have a blue notum with black bands, tubercles capped in yellow, yellow rhinophores, and the foot sole lacking a black stripe. This species can be also distinguished from other phyllidiids by the "Y" shape of the dorsum (Bergh 1905, Brunckhorst 1989, 1993).

Phyllidia ocellata Cuvier, 1804
(Fig. 5)

Phyllidia ocellata Cuvier 1804: 269, pl. 18A, fig. 7, Gray 1857: 216, Gosliner *et al.* 1996: 169, species number 595, Yonow 1996: 485-487, figs. 1A-G, 4A, table 1.

Material examined

RBINS: PNG (41.2 mm × 20.9 mm); Laing Island (31.8 mm × 21.4 mm, 28.2 mm × 18.5 mm).

Description

The dorsal surfaces of preserved specimens are pale in color with black rings. There is a longitudinal median row of five rounded tubercles that are joined by a small crest (Fig. 5A); the anal opening is located behind this crest. These tubercles are narrowed at their bases and have a rough surface. Anterior to the rhinophores on the midline there is a tubercle surrounded by a black ring. On either side of the midline row there are two black rings, which may be complete or semicircular. On the mantle margins there are small rounded tubercles and in one specimen there are also some small black spots on the posterior region of the dorsum. The rhinophores are pale; next to each one is a rhinotubercle. Ventrally, the sole has no black line and the oral tentacles are separate (Fig. 5B).

The pharyngeal bulb (Fig. 5C) has oral glands (some of them are long). The pharyngeal retractor muscles insert posteriorly and dorsally onto the bulb. The pharynx is not very long, arises posteriorly from the pharyngeal bulb (Fig. 5D), and passes through the central nerve ring. The esophagus is narrow and inserts on the anterior end of the digestive gland. The intestine originates to the left of the pericardium, turns to the right, and extends to the anal papilla. The reproductive system (Fig. 5E) has a rounded ampulla. The prostate narrows into a narrow and coiled vas deferens. The bursa copulatrix is spherical and is connected by a narrow duct to the receptaculum seminis, which is slightly oval.

Remarks

The specimens studied in this paper exhibit the typical dorsal pattern for *Phyllidia ocellata* (Brunckhorst 1993,

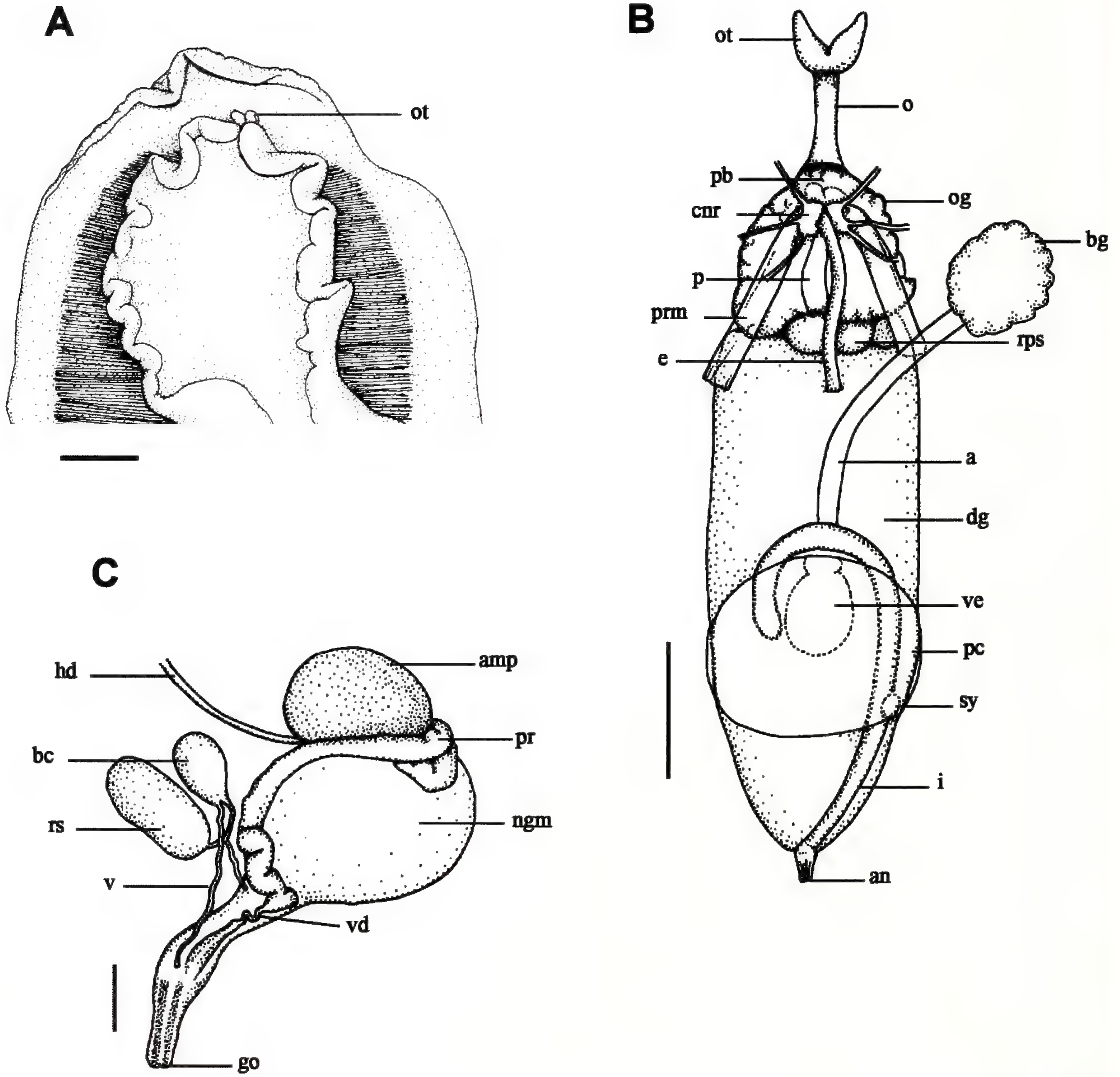

Figure 4. *Phyllidia coelestis.* A, Drawing of the ventral view of the anterior end of a preserved specimen 30.9 mm long, collected in PNG. B, Diagram of the internal anatomy. C, Diagram of the dorsal view of the reproductive system (the same specimen illustrated in Fig. 4A). Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; go, genital opening; hd, hermaphrodite duct; i, intestine; ngm, nidamental gland mass; o, oral tube; og, oral gland; ot, oral tentacles; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; prm, pharyngeal retractor muscle; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 5 mm (A, B), 1 mm (C).

Yonow 1996), having five black rings encircling a tubercle; the tubercles have a rough surface and they are aligned along the median dorsal surface, forming a crest.

One animal studied in the preserved state has incomplete rings on the posterior area of the dorsum; it may have lost its black pigment.

Phyllidia picta Pruvot-Fol, 1957
(Fig. 6)

Phyllidia picta Pruvot-Fol 1957: 110, figs. 5-12.
Fryeria rueppelli Baba and Hamatani 1975: 178-179, fig. 5.
Fryeria menindie Brunckhorst 1993: 47-49, fig. 26B, pls. 4G, 5A.
Fryeria picta Yonow 1996: 511-513, figs. 14A-K, table 3.

Material examined

Expedition 1996: Laing Island, 0.5 m depth (25.6 mm × 12.1 mm, 24.8 mm × 11.4 mm).

Description

The body is elongate-ovate in shape and the notum is black with large rounded tubercles near the midline. These tubercles are aligned into three longitudinal rows (Fig. 6A). The midline row is formed by four isolated tubercles (anterior to the rhinophores there is a smaller one). The other two rows are located on either side of the central ridge: Each is formed by 3-4 tubercles that begin posterior to the rhinophore. The rhinophores are pale in color. Between these tubercles there is a short, narrow, longitudinal crest or a series of smaller black tubercles. Pale semicircles with tubercles occur around the mantle margins. These areas have small black spots in some specimens. The oral tentacles are triangular in the preserved state (Fig. 6B). The anus is located ventrally posterior to the edge of the foot (Fig. 6C).

The oral tube is short and has a pale transverse black band on its base (Fig. 6D). The pharyngeal bulb (Fig. 6E) has oral glands on its surface. The pharyngeal retractor muscles insert posteriorly and dorsally onto the bulb near the area where the long pharynx arises. The pharynx narrows and passes through the central nerve ring. It connects to a thick esophagus that inserts into the digestive gland. The intestine originates to the left of the pericardium, turns to the right, and extends to the anal papilla, which opens ventrally. The reproductive system (Fig. 6F) has a large ampulla; the slightly folded prostate connects with the vas deferens. The bursa copulatrix is spherical and connects with the larger receptaculum seminis. Near the bursa copulatrix the vaginal duct is wide; distally it is narrower.

Remarks

Pruvot-Fol (1957) was the first author to describe this species, which she assigned to the genus *Phyllidia*. This species, however, differs from the type of this genus in several ways, including the location of the ventral anus. Later it was assigned to the genus *Fryeria* (Yonow 1996). Brunckhorst (1993) redescribed the genus *Fryeria*, which in his opinion is distinct from *Phyllidia*. However, with the exception of the position of the anus, Valdés and Gosliner (1999) did not find other consistent differences between *Fryeria* and *Phyllidia*, and consequently synonymized these two names.

Externally, *Phyllidia picta* resembles *Phyllidia coelestis* in its pattern and coloration of tubercles. Individuals of *P. picta* can also be confused with other species such as *Phyllidia rueppelli* (Bergh, 1869) because both have rows of isolated tubercles on the dorsum and semicircles of pale notum on the margin, but the mantle of *P. rueppelli* is edged in yellow-orange and is only known from the Red Sea (Yonow 1986, Brunckhorst 1993, Fahrner and Beck 2000). Individuals of *P. picta* also resemble those of *Phyllidia marindica* (Yonow and Hayward, 1991), but this species has a dorsal midline ridge and numerous short black lines on the mantle margin that extend toward the edge.

Phyllidiopsis shireenae Brunckhorst, 1990
(Fig. 7)

Phyllidia sp. Brunckhorst 1989: 7 (color illustration).
Phyllidiopsis shireenae Brunckhorst 1990b: 577-583, figs. 1-4; Brunckhorst 1993: 66-67, figs. 29F-G, pl. 8B, Fahrner and Beck 2000: 200, pl. 1, fig. 5.

Material examined

RBINS: PNG (64.4 mm × 28.5 mm, 59.2 mm × 32.5 mm, 75.5 mm × 32.2 mm, 61.0 mm × 30.2 mm, 69.5 mm × 25.5 mm, 57.0 mm × 24.1 mm, 24.1 mm × 7.4 mm); Laing Island (61.0 mm × 24.9 mm, 64.1 mm × 21.7 mm, 46.0 mm × 17.9 mm, 65.3 mm × 36.3 mm).

Description

The dorsal surface is pale in color with a longitudinal median crest that is continuous, high, and triangular in cross-section (Fig. 7A). The crest can be seen in living and preserved specimens. Posterior to each pale-colored rhinophore is a longitudinal row of simple angular tubercles. A black band surrounds the median part of the dorsum that encloses the rhinophores and the anus; the latter is located at the posterior end of the median ridge. On the mantle margin there are transverse black lines radiating from the black ring that extend toward the edges of the mantle, one anterior, one posterior, and one or two laterals. Some preserved specimens appear faded and seem to have lost the black pigmentation. In some specimens the median crest has a dark spot or a row of spots. One specimen also has a small transverse black line on the dorsum. Ventrally (Fig. 7B), there is a black

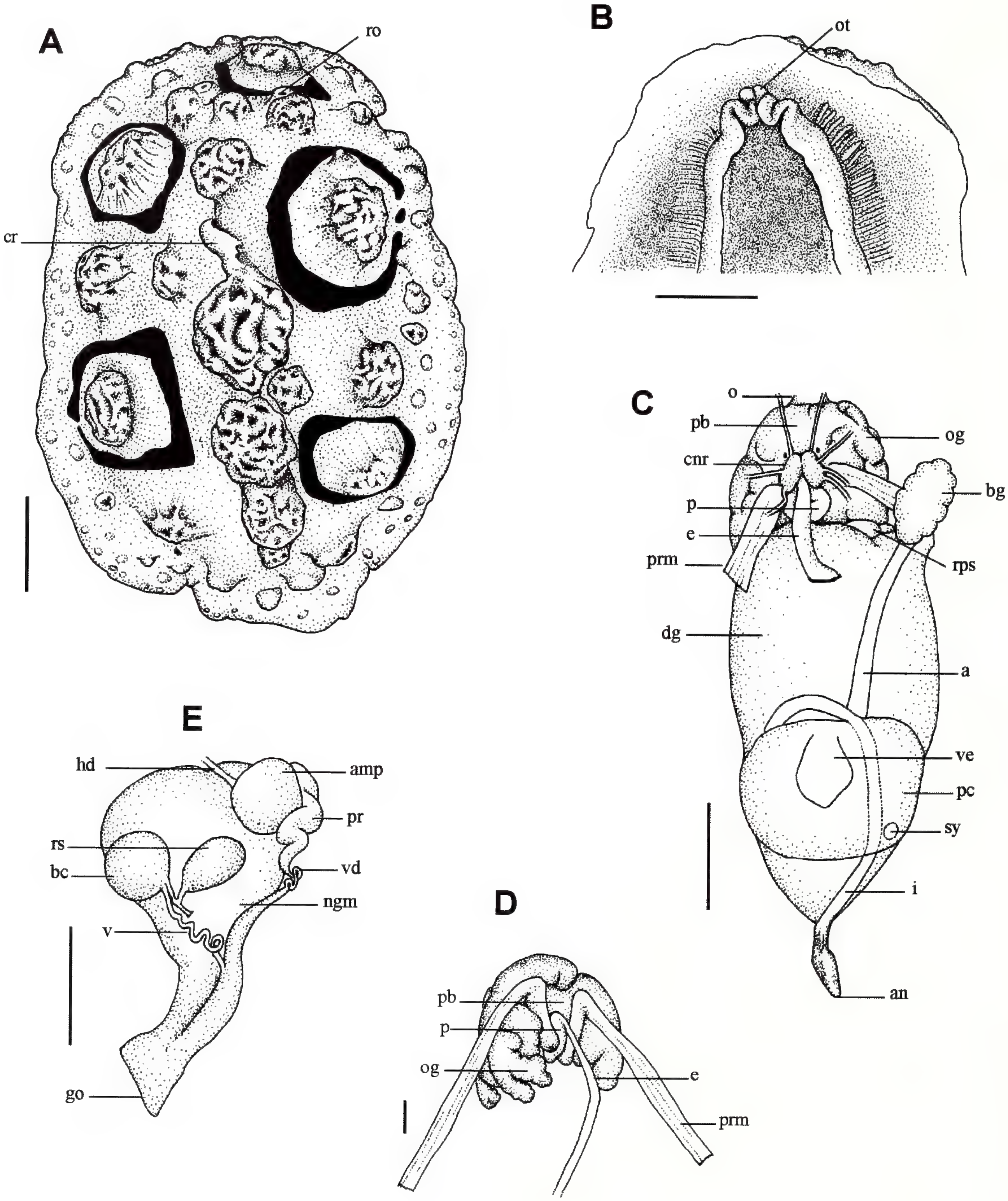
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Figure 5. *Phyllidia ocellata.* A, Drawing of the dorsal view of a preserved specimen 31.8 mm long, collected in Laing Island. B, Drawing of the ventral view of the anterior end (the same specimen illustrated in Fig. 5A). C, Diagram of the internal anatomy of a specimen 28.2 mm long collected in Laing Island. D, Diagram of the dorsal view of the pharyngeal bulb of a specimen 41.2 mm long collected in PNG. E, Diagram of the dorsal view of the reproductive system. Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; cr, crest; dg, digestive gland; e, esophagus; go, genital opening; hd, hermaphrodite duct; i, intestine; ngm, nidamental gland mass; o, oral tube; og, oral gland; ot, oral tentacle; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; prm, pharyngeal retractor muscle; ro, rhinophoral opening; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 5 mm (A, B, C), 2 mm (D, E).

stripe on either side of the foot where it meets the gills. The broad oral tentacles are fused and have rounded tips.

The oral tube can be broad or long and narrow. The pharynx is very long, thick, and passes through the central nerve ring (Fig. 7F). The esophagus has a long segment where the buccal ganglia insert, and posteriorly a shorter segment which has circular musculature. In this area insert the esophageal retractor muscles. In three specimens, the posterior end of the esophagus was broad and rounded (Fig. 7C). In the rest of the specimens, the esophagus is "U" shaped and there is a long region with circular musculature and another segment lacking musculature that inserts into the digestive gland (Fig. 7D). The intestine arises from the digestive gland to the left of the pericardium. It turns to the right and extends to the long anal papilla. The reproductive system (Fig. 7E) has a large ampulla partially covered by the prostate. The prostate is long, very coiled, and bound by connective tissue. The bursa copulatrix is large, spherical, and communicates with the smaller oval receptaculum seminis.

Remarks

Phyllidiopsis shireenae has characters in common with two other species belonging to the genus *Phyllidiopsis*: *Phyllidiopsis krempfi* Pruvot-Fol, 1957 and *Phyllidiopsis pipeki* Brunckhorst, 1993. These species have pink dorsal surfaces with black lines and large tubercles, but *P. shireenae* differs from the other two species by having a median crest that is triangular in cross-section, angular tubercles, pink rhinophores, and ventral black bands. *Phyllidiopsis krempfi* and *P. pipeki* have compound or multi-compound tubercles and their rhinophores are black and pink.

We have observed that the external morphological features of *Phyllidiopsis shireenae* are constant but the internal morphology can vary. Most of the specimens studied have rounded esophagi (Fig. 7C) but in three individuals this structure is longer (Fig. 7D).

Phyllidiopsis cardinalis Bergh, 1875
(Fig. 8)

Phyllidiopsis cardinalis Bergh 1875: 670-673, pl. 16, figs. 11-15, Eliot 1904: 284, Dawydoff 1952: 111, Pruvot-Fol 1957: 118-120, fig. 35, Burn 1975: 516, Gosliner and Behrens 1988: 308-309, 312-313, figs. 1B, 3, Brunckhorst 1993: 63-64, figs. 10A-C, 14, 15, pl. 7E-F, Valdés and Gosliner 1999: 319, figs. 1D, 2F, 3F, 4E, 5D, 6D, 10B, 14C, 15C, 20D, 22B, Yonow *et al.* 2002: 869-870, fig. 19B.

Phyllidia tuberculata Risbec 1928: 59-60, fig. 3, pl. 1, fig. 2.

Material examined

RBINS: PNG (20.3 mm × 10.1 mm).

Description

The median region of the dorsal surface has three longitudinal rows of isolated, compound tubercles, most of which are large and globose (Fig. 8A). The midline row is formed by five tubercles: it begins posterior to the rhinophores and extends to the anal opening. On either side of the midline there is another row, each one formed by three tubercles. On the mantle margin there are compound rounded tubercles, and around the edge there are black spots. In the preserved state, the entire body is reddish, as are the rhinophores. The rim of the rhinophoral pocket has a black stain. On the sides of the foot, near the edge, there are small isolated black spots (Fig. 8B). The oral tentacles are fused together.

Phyllidiopsis cardinalis has a long, thick pharyngeal bulb that is displaced towards the left side of the body (Fig. 8C). The pharynx passes through the central nerve ring. At the anterior end of the pharynx are a pair of ganglia that are connected with the central nerve ring. The esophagus is reinforced by circular muscles in the region of the esophageal retractor muscles, and inserts into the digestive gland mass. The intestine exits the gland, turns to the right, and extends to the anal papilla. The reproductive system (Fig. 8D) has a large, oval ampulla that is located next to a folded prostate. The penial sheath is wide and long. The receptaculum seminis is small and rounded; it is connected to the larger bursa copulatrix.

Remarks

Phyllidiopsis cardinalis has a complex, multicolored dorsum, completely different from any other known phyllidiid

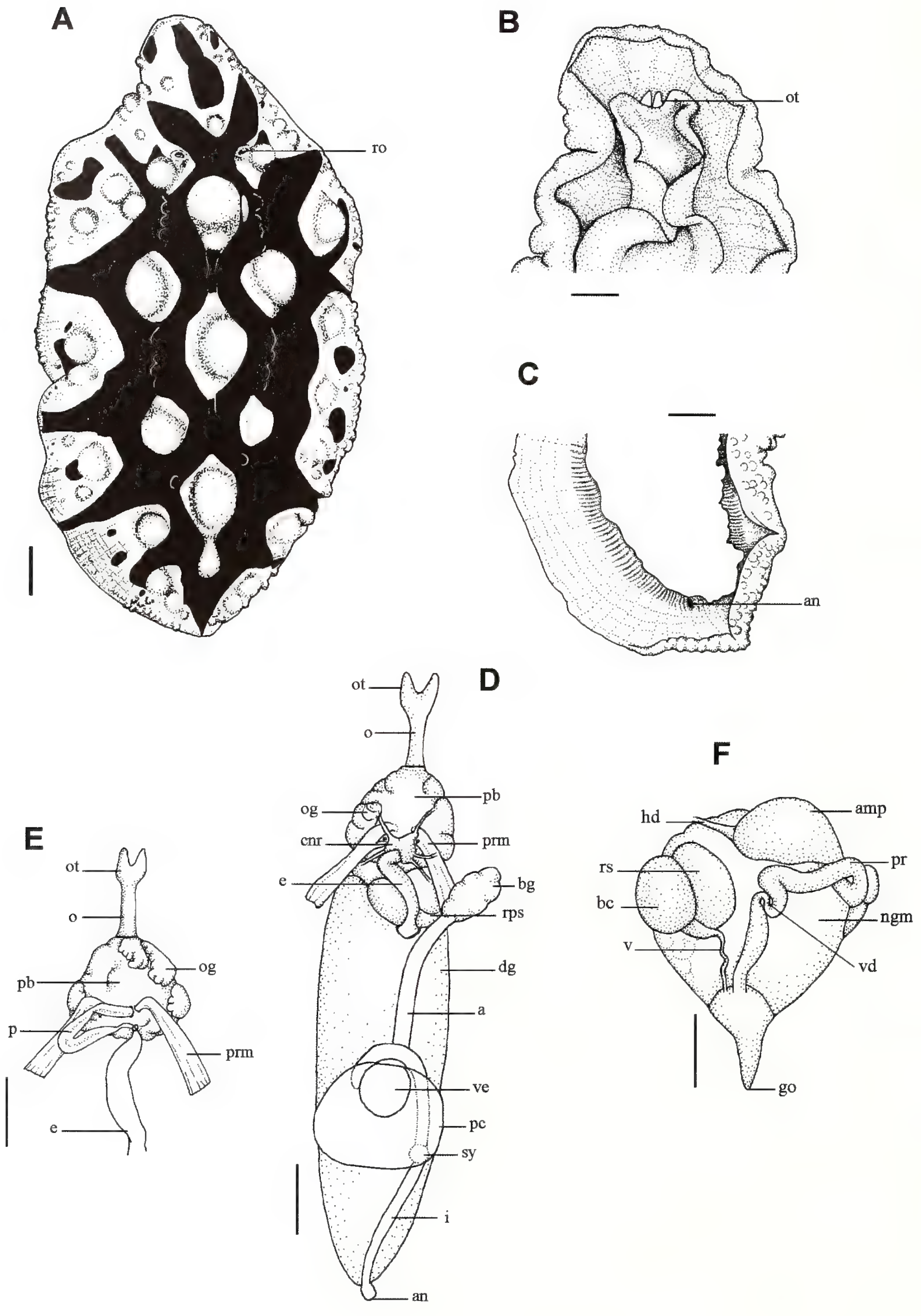
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Figure 6. *Phyllidia picta*. A, Drawing of the dorsal view of a preserved specimen 25.6 mm long, collected in Laing Island, depth 0.5 m. B, Drawing of the ventral view of the anterior end of a preserved specimen 24.8 mm long, collected in Laing Island, depth 0.5 m, showing the oral tentacles. C, Drawing of the ventral view of the posterior end (the same specimen illustrated in the figure 6B), showing the anal opening. D, Diagram of the internal anatomy. E, Diagram of the dorsal view of the pharyngeal bulb (the same specimen illustrated in Fig. 6A). F, Diagram of the dorsal view of the reproductive system (the same specimen illustrated in Fig. 6A). Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; go, genital opening; hd, hermaphrodite duct; i, intestine; ngm, nidamental gland mass; o, oral tube; og, oral gland; ot, oral tentacles; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; prm, pharyngeal retractor muscle; ro, rhinophoral opening; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 2 mm (A, B, C, D, E), 1 mm (F).

species (Brunckhorst 1993). The specimen studied appears faded, but its identification is possible because of other characters, such as the presence of large, globose, compound tubercles on the median dorsum, which in this specimen are arranged in three longitudinal rows, instead of the two rows mentioned by Brunckhorst (1993). There are also small rounded tubercles and dark spots around the margin. On the sides of the foot there are dark spots and the oral tentacles are fused. *Phyllidiopsis krempfi* Pruvot-Fol, 1957 also has large compound tubercles on the central dorsum, but its general coloration is pale pink and it has black lines.

Phyllidiopsis krempfi Pruvot-Fol, 1957
(Figs. 1E-F, 9)

Phyllidiopsis krempfi Pruvot-Fol 1957: 120-121, figs. 41-49, pl. 1, figs. 7-8, Brunckhorst 1993: 66, fig. 29E, pl. 8A, Fahrner and Beck 2000: 200.

Material examined

Expedition 1996: Boisa Island, 56.4 m depth (36.6 mm × 16.9 mm).

Description

The ground color of the dorsum is pink, with compound tubercles with pink bases and white apices (Fig. 1E). In the median region of the dorsum there are three longitudinal rows of tubercles that can be isolated or joined at their bases. The tubercles on the edge of the mantle are single, rounded, and very small. On either side of the median region there is a longitudinal black line (in this specimen the right line is longer than the left), and both meet anterior to the rhinophores and extend posteriorly in a line to the margin. At the margin there are two transverse black rays on either side. Short black rays and blotches occur between some tubercles and on the mantle margins. The rhinophores are pink at their bases and their anterior surfaces. They have black apices and black posterior surface. Ventrally, the hyponotum is pink. The gills are dark in color and the pedal sole is pinkish-grey (Fig. 1F). The broad oral tentacles are fused and pink.

The oral tube has a thin wall. On either side of the pharyngeal bulb arise narrow pharyngeal retractor muscles (Fig. 9A). The pharynx extends from the posterior part of the bulb and passes through the central nerve ring. The buccal ganglia are situated on the surface of the pharynx. The muscular esophagus is longer than the pharynx. The esophagus has a longer segment that extends near the pericardium and turns forming a "U." In this area insert the esophageal retractor muscles. The esophagus has another segment that is shorter and stouter, and inserts into the digestive gland. The intestine arises to the left of the pericardium, turns to the right, and extends to the narrow anal papilla. The reproductive system (Fig. 9B) has a large and oval ampulla that is connected with the folded prostate. The prostate is bound together by connective tissue. The bursa copulatrix is very large and spherical and the receptaculum seminis is rounded and smaller.

Remarks

It is very difficult to distinguish between *Phyllidiopsis krempfi* and *Phyllidiopsis pipeki* Brunckhorst, 1993, because both species possess very similar characteristics. According to Brunckhorst (1993), individuals in both species have pink dorsal surfaces (according to Fahrner and Beck [2000] the dorsal surface of *P. pipeki* is cream in color), with tubercles that have wide pink bases and the dorsum has two primary longitudinal black lines. Both species have shorter lines extending to the mantle edges and sometimes have black marks and spots, the rhinophores are pink and black, and the coloration is pink and pale grey ventrally, with pink fused oral tentacles. The main difference between these species is that *P. pipeki* can have single or compound tubercles with white rounded apices, but *P. krempfi* has more numerous, compound tubercles with pale pink apices (Brunckhorst 1993). Internally, *P. pipeki* has a longer and wider muscular segment of the esophagus. The region that inserts into the digestive gland is wider and has less musculature than that of *P. krempfi*. The reproductive systems of both species are similar.

Phyllidiopsis pipeki Brunckhorst, 1993
(Fig. 10)

Phyllidiopsis pipeki Brunckhorst 1993: 73, fig. 30B, pl. 9A, Debelius 1996: 269, Marshall and Willan 1999: 128, fig. 231, Fahrner and Beck 2000: 200, pl. 1, fig. 3.

Phyllidia nobilis Lim and Chou 1970: 134, pl. 16, fig. A.

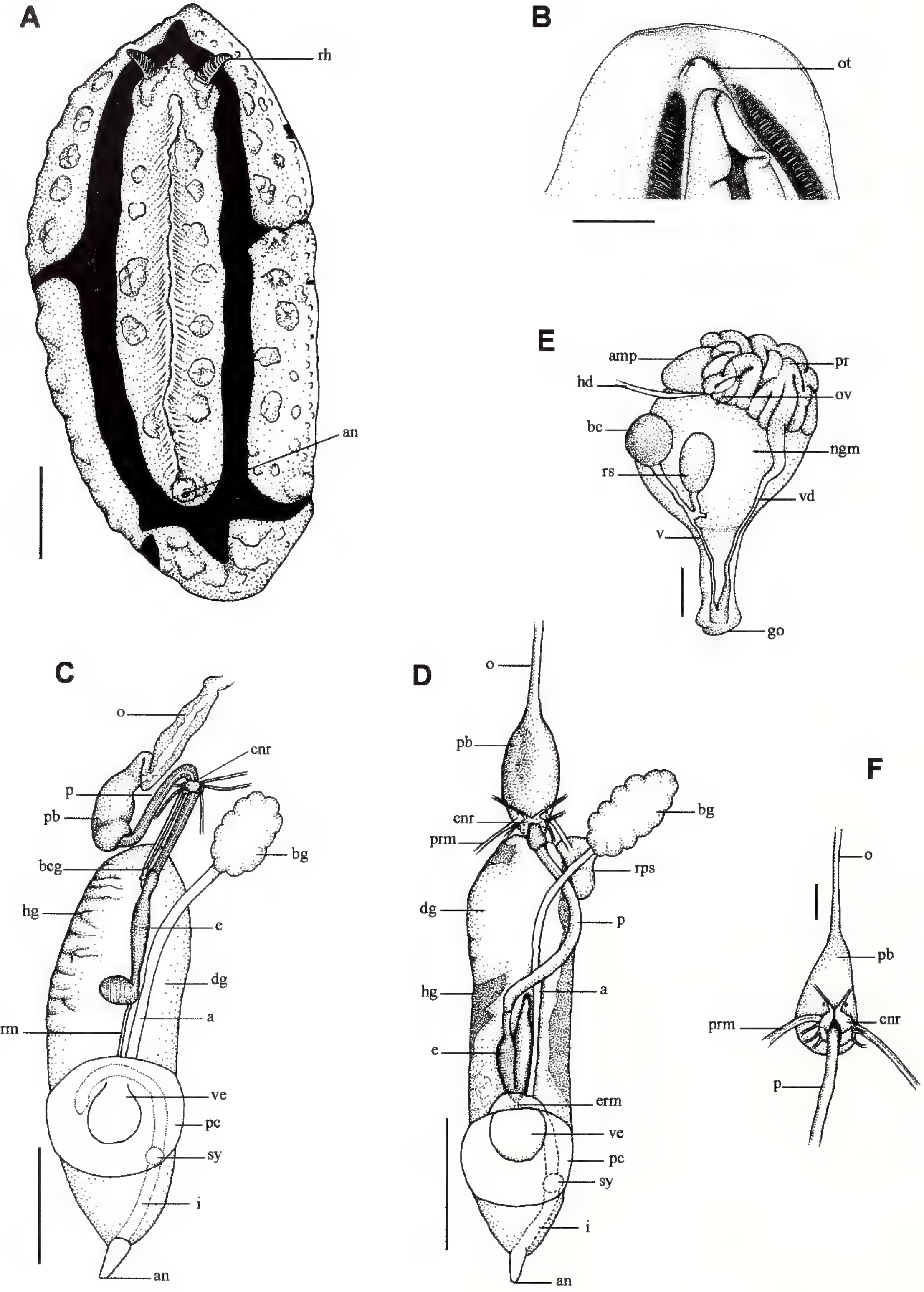
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Figure 7. *Phyllidiopsis shireenae*. A, Drawing of the dorsal view of a preserved specimen 65.3 mm long, collected in Laing Island. B, Drawing of the ventral view of the anterior end (the same specimen illustrated in Fig. 7A), in ventral view. C, Diagram of the internal anatomy (the same specimen illustrated in Fig. 7A), showing how the esophagus ends with a broad rounded region. D, Diagram of the anatomy of a specimen 64.4 mm long, collected in PNG, with the esophagus forming a "U." E, Diagram of the dorsal view of the reproductive system (the same specimen illustrated in Fig. 7A). F, Diagram of the dorsal view of the pharyngeal bulb of a specimen 59.2 mm long, collected in PNG. Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; bcg, buccal ganglia; cnr, central nerve ring; dg, digestive gland; e, esophagus; erm, esophageal retractor muscle; go, genital opening; hd, hermaphrodite duct; hg, hermaphrodite gland; i, intestine; ngm, nidamental gland mass; o, oral tube; ot, oral tentacle; ov, oviduct; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; prm, pharyngeal retractor muscle; rh, rhinophore; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 10 mm (A, B, C, D), 2 mm (E, F).

Material examined

RBINS: PNG (32.3 mm × 12.5 mm).

Description

The dorsum is pale in color. This specimen has two longitudinal black lines that merge anterior to the rhinophores (Fig. 10A) and black lines extending to the mantle edge (one anterior, two on one side and three on the other). The tubercles in the median area are large and compound but are not tall, nor do they form ridges. The apices of the tubercles are paler than the bases. On the mantle margin the tubercles are complex and near the edge they are single, very small, and rounded. The rhinophores are black at the apices and on their posterior surfaces. Their anterior faces are pale in color. In preserved specimens the ventral surface is pale except for the gills, which are dark grey. The oral tentacles are fused and their tips are rounded (Fig. 10B).

The large pharyngeal bulb is folded. The pharynx extends toward the right side, turns to the anterior region of the digestive gland, and passes through the central nerve ring (Fig. 10D). Two sack-shaped structures arise from the bulb and extend to the nerve ring. The anterior portion of the esophagus is short. The mid-esophagus is very long, thick, and reinforced with circular muscles. This segment extends near the pericardium and turns, forming a "U." In this area insert the esophageal retractor muscles. The next region of the esophagus is shorter, stouter, and inserts into the digestive gland (Fig. 10C). The intestine arises to the left of the pericardium, turns to the right and extends to the anal papilla. The reproductive system (Fig. 10E) has a large and compact prostate that is bound together by connective tissue. The bursa copulatrix is spherical and very large. It is connected to a smaller receptaculum seminis and to the vaginal duct.

Remarks

Phyllidiopsis pipeki is very similar to *Phyllidiopsis krempfi*. The differences between these species are mentioned in the discussion of *P. krempfi* above.

Phyllidiella pustulosa (Cuvier, 1804)
(Figs. 1G-I, 11)

Phyllidia pustulosa Cuvier 1804: 268, pl. A, fig. 8.
Phyllidia nobilis Risbec 1928: 58.
Phyllidia melanocera Yonow 1986: 1406-1407, figs. 2, 10F-I.
Phyllidiella pustulosa Brunckhorst 1993: 49-54, figs. 3B, 9B-D, 11-13, 27, 28A-C, pl. 5E-F, Gosliner *et al.* 1996: 169, species number 597, Marshall and Willan 1999: 125-126, fig. 227, Fahrner and Beck 2000: 201, pl. 2, fig. 3, Valdés 2001: 339-341, figs. 1B, 5B-C, 6.

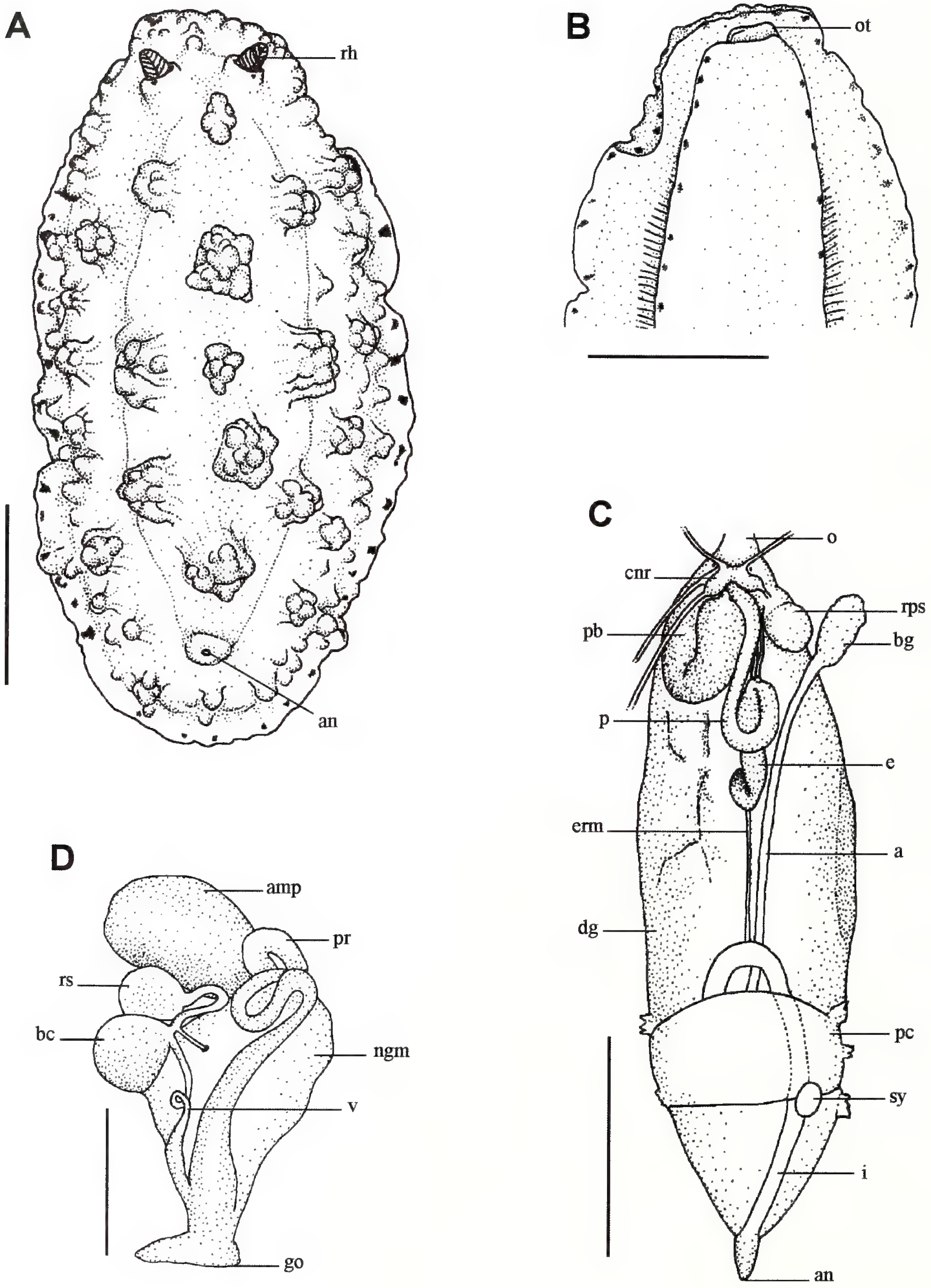
Material examined

RBINS: PNG (32.3 mm × 15.0 mm, 32.8 mm × 11.5 mm, 47.8 mm × 20.7 mm, 36.5 mm × 12.9 mm, 40.0 mm × 15.1 mm, 37.9 mm × 15.2 mm, 13.4 mm × 6.2 mm, 28.5 mm × 9.1 mm, 28.0 mm × 11.2 mm, 30.3 mm × 10.9 mm, 16.8 mm × 5.4 mm, 12.3 mm × 5.0 mm, 28.5 mm × 10.4 mm, 20.3 mm × 7.7 mm, 20.2 mm × 8.1 mm, 24.6 mm × 7.5 mm, 18.9 mm × 9.0 mm); Laing Island (23.0 mm × 10.0 mm, 24.6 mm × 12.8 mm, 19.4 mm × 13.0 mm, 26.3 mm × 10.1 mm, 23.2 mm × 14.5 mm, 13.8 mm × 6.8 mm, 24.0 mm × 14.8 mm); Durangit Reef, 40 m depth (27.4 mm × 13.2 mm), Ilot Tabou (41.0 mm × 18.8 mm).

Expedition 1996: Laing Island, 0.5 m depth (44.1 mm × 19.0 mm, 30.5 mm × 10.8 mm, 27.1 mm × 10.9 mm, 43.1 mm × 19.4 mm, 25.8 mm × 14.2 mm, 26.6 mm × 11.2 mm, 18.2 mm × 11.6 mm, 24.3 mm × 14.4 mm, 23.9 mm × 14.07 mm), Laing Island, 14.1 m depth (25.4 mm × 7.6 mm, 21.9 mm × 7.6 mm, 14.6 mm × 6.4 mm); Laing Island, 15 m depth (31.2 mm × 10.5 mm, 15.6 mm × 5.8 mm, 15.1 mm × 5.0 mm); Laing Island, 15.7 m depth (14.0 mm × 5.5 mm, 8.7 mm × 3.4 mm); Laing Island, 16.5 m depth (30.5 mm × 12.6 mm, 25.6 mm × 8.6 mm); Laing Island, 16.7 m depth (28.8 mm × 11.2 mm, 25.8 mm × 10.8 mm); Laing Island, 18.5 m depth (23.6 mm × 7.9 mm, 12.4 mm × 4.5 mm); Laing Island, 45 m depth (25.6 mm × 12.9 mm, 10.8 mm × 3.5 mm); Hansa Bay, 20-28.9 m depth (22.8 mm × 12.9 mm, 14.1 mm × 5.1 mm).

Description

The dorsal surface is black and the tubercles are pink with paler pink apices, although some specimens were green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when they were collected. The tubercles may be single or compound and are fused to form small groups. The largest specimens (Fig. 1G) have three regions (median, lateral, and marginal) separated by black notum. These regions have tubercles organized in clusters: The median region has three groups—anterior, median, and posterior—and the anus is located posterior to the third group. In the lateral region the clusters are separated by black notum and the marginal region is occupied by small single tubercles. The edges of the mantle of most specimens are narrow and pink, although in some specimens there are areas occupied by black notum. Each of the specimens of medium size (Fig. 1H) has a median region and a lateral region with clusters of tubercles separated by a black notum. In the median region there are three groups (anterior, median, and posterior) between the rhinophores and the anus, although in some animals the groups are not very well defined. The mantle edge is pink. Eleven specimens are juveniles (Fig. 1I), ranging in length from 8.7-16.8 mm; they have three groups of tubercles in the median region that are separated by black lines. Some of the groups have black irregular marks on their centers. The lateral tubercles are separated from the mantle edge by a black line. The mantle edge is pink. The rhinophores are black, however, in the preserved state some rhinophores are paler at their bases. The hyponotum and the pedal sole are grey (Fig. 11A). Dorsally the foot is dark grey. In many specimens the oral tentacles have dark tips.

The oral tube is wide (Fig. 11B) and the thick pharyngeal bulb is slightly folded. On the posterior part of bulb are numerous oral glands that are relatively large. Each gland is joined to the bulb by a short stalk. The pharynx is large and broad at its origin at the pharyngeal bulb, but it narrows as it passes across the central nerve ring. The esophagus is very thin and inserts into the anterior region of the digestive gland. The reproductive system (Fig. 11C) has a large oval ampulla that is brownish-yellow. The prostate is long and folded. The bursa copulatrix is large and oval. It is connected to the small, dark receptaculum seminis by a duct.

Remarks

Underwater the tubercles appear grey or green. This fact has been commented by other authors, such as Brunckhorst (1993). Some preserved specimens have black rhinophores with paler bases. Four specimens are very faded and appear to have lost the black pigmentation of the notum, but they could be identified by the arrangement of tubercles, the black rhinophores, and their anatomical details.

One example of ontogenetic variability which has given room to misidentification is that of *Phyllidiella pustulosa* (see Brunckhorst 1993). There are external differences between the adults and the young specimens because juveniles have tubercles grouped in amalgamated clusters and large animals have separated tubercles (Fig. 1G-I, Brunckhorst 1993, Fahrner and Beck 2000). However, all specimens have black dorsal surfaces with pink single or compound tubercles that may be fused to form small groups. On the median region of the dorsum there are three groups of tubercles (anterior, median, and posterior), and the mantle edge is pink. The rhinophores are black. Internally there are numerous large oral glands; each gland is joined to the pharyngeal bulb by a short stalk.

Phyllidiella zeylanica (Kelaart, 1858)
(Fig. 12)

Phyllidia zeylanica Kelaart 1858: 120.

Phyllidiella zeylanica Brunckhorst 1993: 57-58, pl. 6E-G, Yonow 1996: 502-504, figs. 10A-G, Debelius 1996: 267, Fahrner and Beck 2000: 201, pl. 1, fig. 6, Yonow *et al.* 2002: 868, fig. 19A.

Material examined

RBINS: PNG (15.2 mm × 6.8 mm); Nossi-Bé (27.0 mm × 9.4 mm, 15.2 mm × 6.8 mm).

Expedition 1996: Hansa Bay, 20 m depth (17.9 mm × 8.1 mm).

Description

When the specimens were collected their coloration was pale pink and black. The tubercles are small and rounded and can be isolated or joined. On the median region of the dorsum there is a central black ring (Fig. 12A) that surrounds a group of low tubercles that are fused. Outside this ring there are rows of coalesced tubercles and another ring that encloses the rhinophores and anus. There is a black line near the pink edge of the mantle. The rhinophores are black. The preserved specimen has triangular oral tentacles (Fig. 12B).

The oral tube is broad (Fig. 12C). The pharyngeal bulb

Figure 8. *Phyllidiopsis cardinalis*. A, Drawing of the dorsal view of a preserved specimen. B, Drawing of the ventral view of a preserved specimen. C, Diagram of the internal anatomy. D, Diagram of the dorsal view of the reproductive system. Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; erm, esophageal retractor muscle; go, genital opening; i, intestine; ngm, nidamental gland mass; o, oral tube; ot, oral tentacle; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; rh, rhinophore; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct. Scale bars = 5 mm (A, B, C), 1 mm (D).

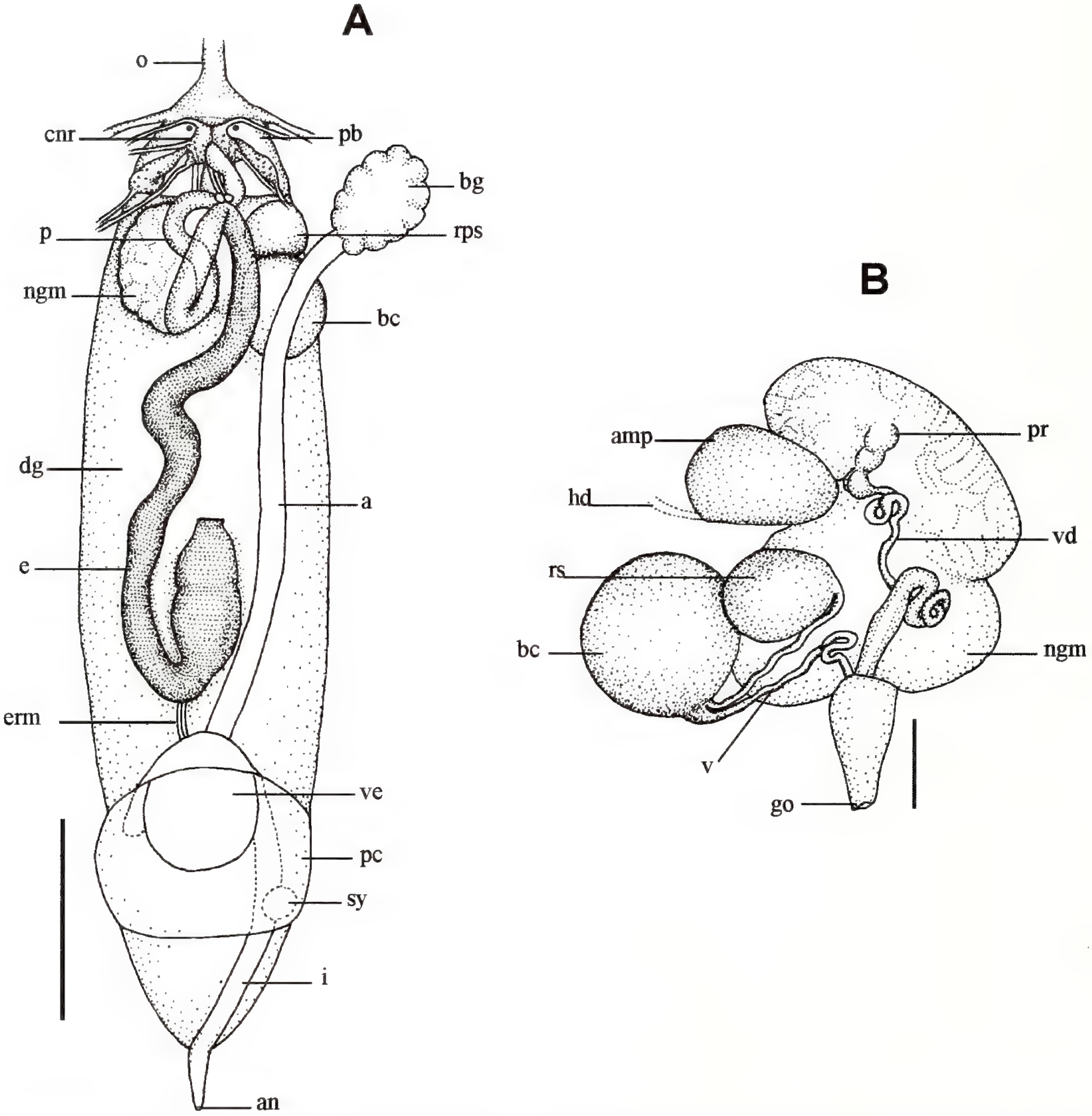
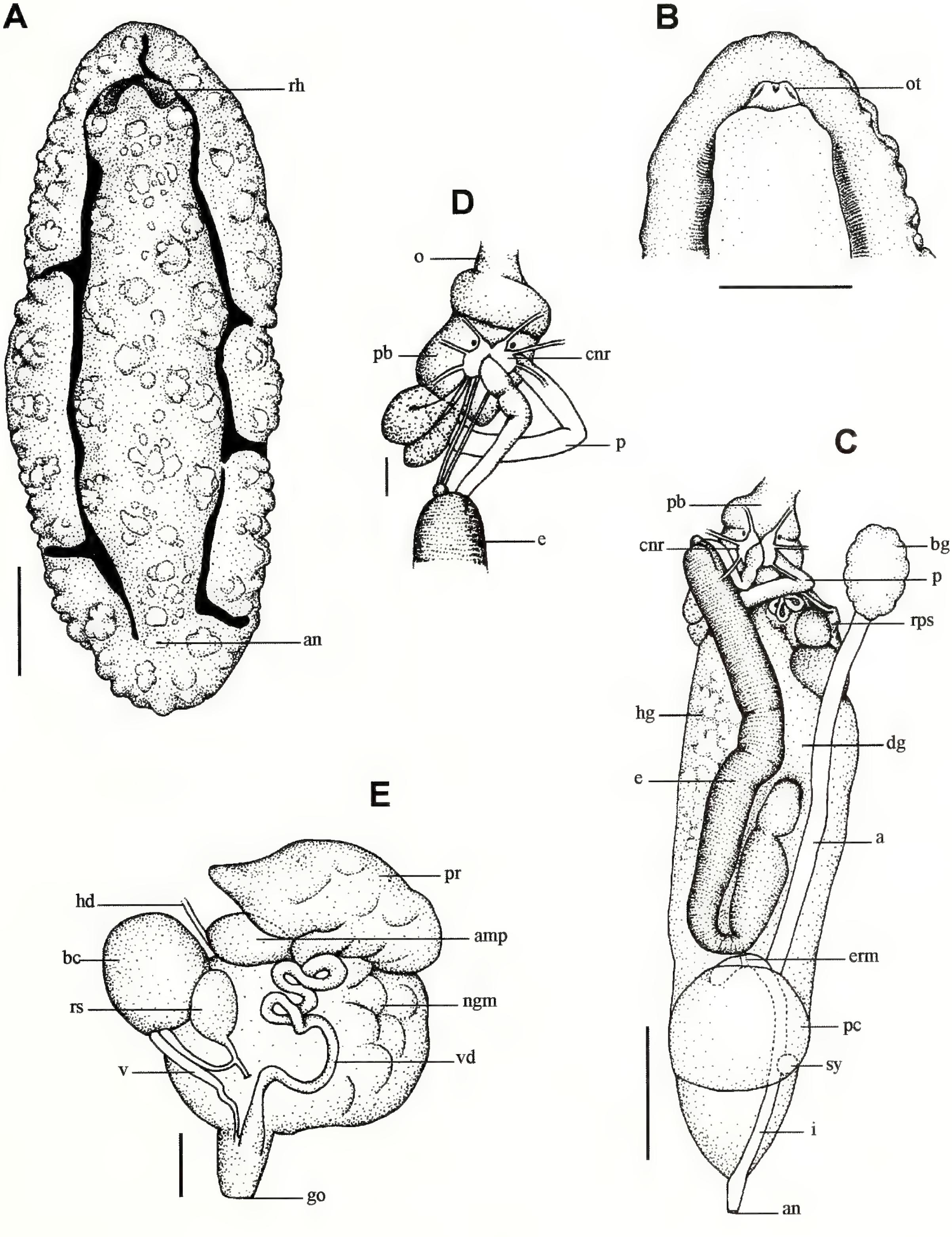


Figure 9. *Phyllidiopsis krempfi*. A, Diagram of the internal anatomy. B, Diagram of the dorsal view of the reproductive system. Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; erm, esophageal retractor muscle; go, genital opening; hd, hermaphrodite duct; i, intestine; ngm, nidamental gland mass; o, oral tube; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 5 mm (A), 1 mm (B).

Figure 10. *Phyllidiopsis pipeki*. A, Drawing of the dorsal view of a preserved specimen. B, Ventral view of the anterior end of a preserved specimen. C, Diagram of the internal anatomy. D, Diagram of the dorsal view of the pharyngeal bulb. E, Diagram of the dorsal view of the reproductive system. Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; erm, esophageal retractor muscle; go, genital opening; hd, hermaphrodite duct; hg, hermaphrodite gland; i, intestine; ngm, nidamental gland mass; o, oral tube; ot, oral tentacle; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; rh, rhinophore; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens. Scale bars = 5 mm (A, B, C), 1 mm (D, E).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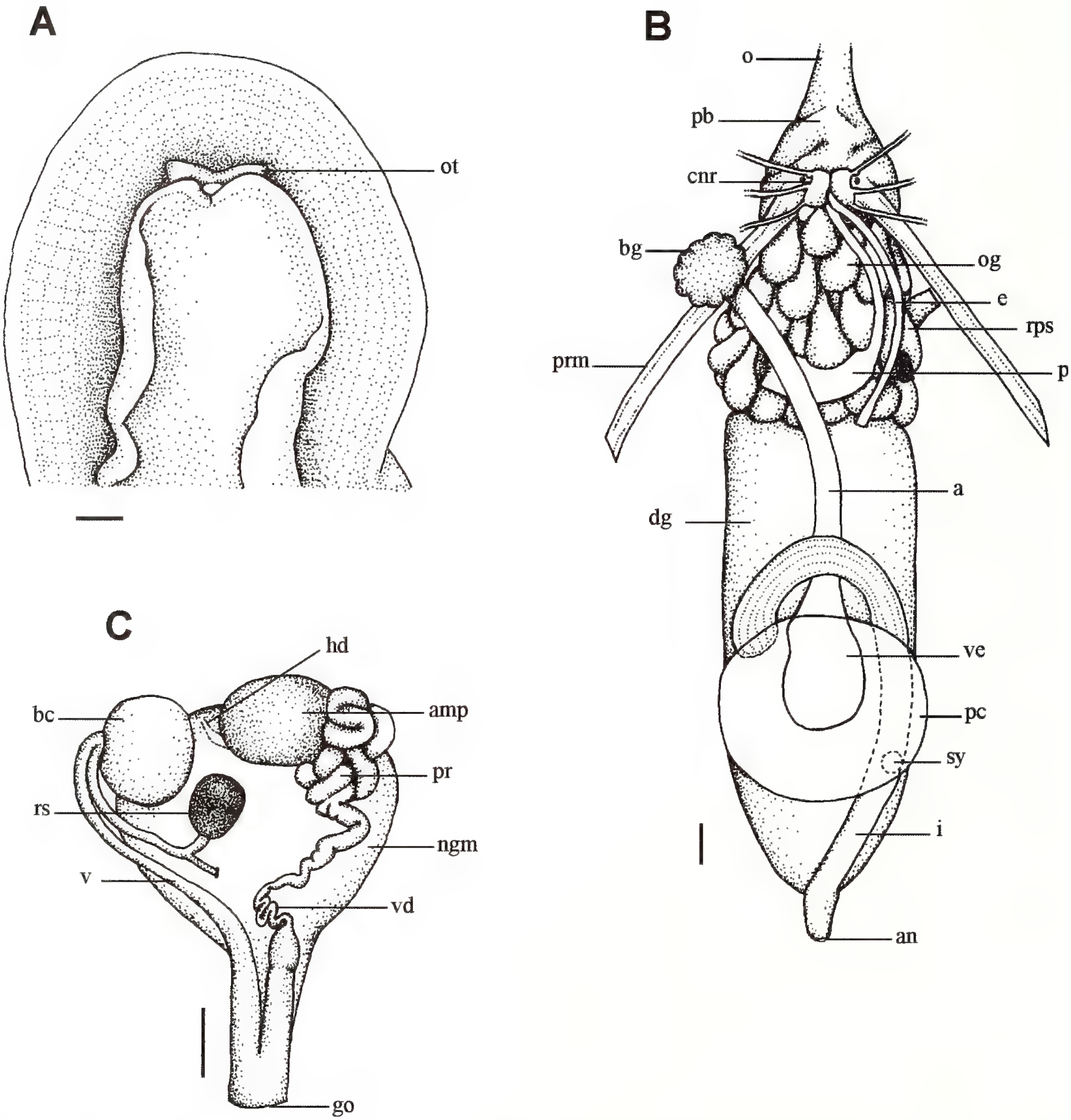

Figure 11. *Phyllidiella pustulosa.* A, Drawing of the ventral view of the anterior end of a preserved specimen 25.4 mm long, collected in Laing Island, depth 14.1 mm. B, Diagram of the internal anatomy of a specimen 30.5 mm long, collected in Laing Island, depth 16.5 m. C, Diagram of the dorsal view of the reproductive system (the same specimen illustrated in Fig. 11B). Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; go, genital opening; hd, hermaphrodite duct; i, intestine; ngm, nidamental gland mass; o, oral tube; og, oral gland; ot, oral tentacle; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; prm, pharyngeal retractor muscle; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 1 mm.

has numerous oral glands that form a large white mass. The pharyngeal retractor muscles are long and insert dorsally into the pharyngeal bulb. The pharynx is broad where it arises from the pharyngeal bulb. It narrows abruptly posteriorly and passes through the central nerve ring. The esophagus is thin and inserts into the digestive gland. The reproductive system (Fig. 12D) has a large, spherical ampulla that is connected to a thick and folded prostate. The bursa copulatrix is large and rounded, and is connected to the small and dark receptaculum seminis by a duct.

Remarks

The most important characteristic of *Phyllidiella zeylanica* is the presence of a pale pink notum with black lines forming concentric rings. This species has black rhinophores and triangular oral tentacles with dark apices. *Phyllidiella zeylanica* shows ontogenetic variation; the juvenile stage has a median mass of fused tubercles. During growth, this mass separates into numerous longitudinal ridges (Brunckhorst 1993). *Phyllidiella pustulosa* also has a pink and black dorsum and black rhinophores, but its tubercles are arranged in groups and the black lines do not form rings. *Phyllidiella rudmani* Brunckhorst, 1993 has a pale pink mantle with only two longitudinal black lines and tubercles organized in longitudinal rows that never form ridges. It has black and pink rhinophores but *P. zeylanica* has completely black rhinophores.

Phyllidiella hageni Fahrner and Beck, 2000
(Figs. 1J, 13)

Phyllidiella hageni Fahrner and Beck 2000: 194-196, figs. 5-7, pl. 1, fig. 8, pl. 2, fig. 1.

Material examined

RBINS: PNG (33.3 mm × 15.6 mm); Laing Island (24.9 mm × 13.4 mm).

Expedition 1996: Laing Island, 16.5 m depth (38.1 mm × 20.1 mm).

Description

Dorsally, the notum is pink in the live animals (Fig. 1J) and white in preserved specimens. Small, white, rounded tubercles, which can be isolated or grouped, are evenly distributed on the dorsum. There are two longitudinal black lines that fuse anterior to the rhinophores and extend separately to the posterior mantle edge (Fig. 13A). In the region of the anus they bend towards the center. In two specimen, the lines turn to the lateral margin again and extend to the mantle edge. In the third specimen one line ends near the anus (Fig. 13B). The animals have several irregular longitudinal short black lines between the two longitudinal lines and on the mantle margins. The mantle edge is black and narrow. The rhinophores have black apices and pink bases. The hyponotum and foot are pale in color. One animal has many rectangular and some triangular gill leaflets. The gills of another specimen are triangular in the posterior region of the body and rectangular in the rest. The third animal has triangular gill leaflets only. In the preserved state the oral tentacles are pale, broad (Fig. 13C), and have a triangular shape.

The oral tube is narrow and long (Fig. 13D). The posterior surface of the pharyngeal bulb is covered by oral glands. The pharyngeal retractor muscles insert dorsally onto the pharyngeal bulb. The short pharynx bends, narrows, and passes through the central nerve ring. The esophagus is longer and inserts into the digestive gland. The reproductive system (Fig. 13E) has an oval ampulla. The prostate is broad and straight. The bursa copulatrix (which is spherical and smaller than the ampulla) is connected by a duct to the receptaculum seminis, which is dark in color in one specimen. From this duct emerges another narrower duct that inserts into the large female gland. The long vagina is connected to the bursa copulatrix.

Remarks

The most distinctive external features of *Phyllidiella hageni* are the pale notum, the numerous single or fused tubercles that are evenly distributed, two longitudinal black lines that converge anterior to the rhinophores, short irregular black lines on the median region and on the margin, a black mantle edge, and black and white rhinophores (Fahrner and Beck 2000).

There are few variations between the dorsal pattern of the studied specimens. The dorsal longitudinal lines bend towards the center, and can turn to the margin again or end near the anus. On the mantle margin there are lines describing a zigzag. Two specimens studied have short variable lines on the median part forming incomplete hexagons, but the other specimens have a few short lines and spots scattered on the dorsum. Ventrally, the gill leaflets can be rectangular, triangular, or individuals can have both forms.

In agreement with Fahrner and Beck (2000) we saw that the receptaculum seminis and the bursa copulatrix have long stalks. Although they observed that the receptaculum seminis of *Phyllidiella hageni* is white and the bursa copulatrix is black, the specimens we examined have black receptaculum seminis and pale bursa copulatrix.

This species is similar in external morphology to *Phyllidiella rudmani*, whose dorsum also has a pink background color with two black longitudinal lines and bicolored rhinophores, but *P. rudmani* has tubercles which can be compound, and they are arranged in rows, the black lines of the dorsum are not connected, and the mantle edge is not black. There are no irregular short lines between the two longitu-

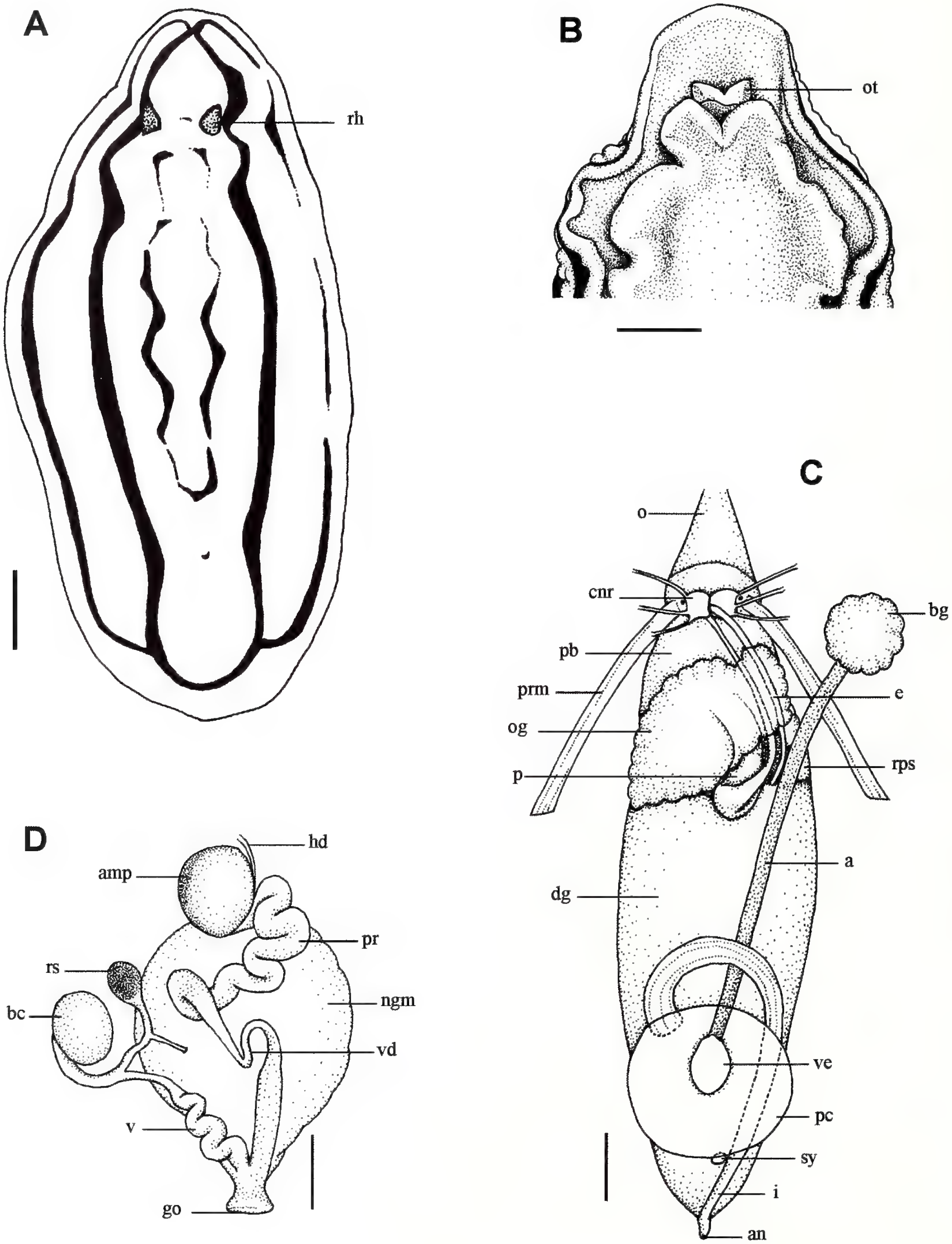
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Figure 12. *Phyllidiella zeylanica.* A, Drawing of the dorsal view of a preserved specimen 17.9 mm long, collected in Hansa Bay (depth 20 m), showing the black rings. B, Drawing of the ventral view of the anterior end of a preserved specimen 27 mm long, collected in Nossi-Bé. C, Diagram of the internal anatomy. D, Diagram of the dorsal view of the reproductive system (the same specimen illustrated in Fig. 12B). Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; go, genital opening; hd, hermaphrodite duct; i, intestine; ngm, nidamental gland mass; o, oral tube; og, oral gland; ot, oral tentacle; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; prm, pharyngeal retractor muscle; rh, rhinophore; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 2 mm (A, B, C), 1 mm (D).

dinal lines and the mantle edge is pink (black in *Phyllidiella hageni*). *Phyllidiella lizae* Brunckhorst, 1993 has a pale pink background with black narrow and irregular lines on the median part of its dorsum, but the rhinophores are black and the mantle edge is pinkish-white.

Phyllidiella backeljaui n. sp.
(Figs. 1K-L, 14)

Material examined

Holotype: Expedition 1996, Laing Island, 9 m depth (20.0 mm × 11.6 mm preserved length), Museo Nacional de Ciencias Naturales of Madrid (MNCN 15.05/46656).

Paratypes: Expedition 1996, Laing Island, 14.1 m depth (24.3 mm × 10.9 mm preserved length), Museo Nacional de Ciencias Naturales of Madrid (MNCN 15.05/46657). RBINS, Laing Island, (23.4 mm × 11.7 mm preserved length), Royal Belgian Institute of Natural Sciences.

Additional material

Expedition 1996: Laing Island, 0.5 m depth (23.0 mm × 12.1 mm). Laing Island, 14.1 m depth (22.2 mm × 11.2 mm).

Etymology

The name *Phyllidiella backeljaui* is in honor of Thierry Backeljau, great malacologist and friend whose endeavors made possible the project in Papua New Guinea in 1996.

Type locality

Laing Island (4°10′30″S, 144°52′47″E), Madang Province, Papua New Guinea. The specimens collected in 1996 were found on the western side of Laing Island.

Description

External anatomy: Body shape elongated and ovate, with a broad mantle (Fig. 1K). Pink dorsal surface, although one specimen was green when collected. Complex tubercles on the median part of dorsum and simple on the mantle margins; their bases have the same color as the notum and the apices are paler. Two longitudinal black bands converge anterior to the rhinophores and extend separately to the posterior region of the dorsum. In the region of the anus they bend towards the center and turn to the margin again. These two lines are connected by a transverse black line that delimits an anterior and a posterior area. These areas have one or two irregular blotches in their centers, black lines crossing over each other forming an "X," or a reticule separating groups of tubercles (Figs. 14A, B). Transverse black lines on margins that delimit semicircles occupied by tubercles and one spot or line. Black and narrow mantle edge. Black rhinophores, although in preserved state the anterior surfaces of their bases are paler. Foot notched anteriorly and grey ventrally (Fig. 1L). The gills are dark and some specimens have rectangular gill leaflets. The oral tentacles have rounded tips (Fig. 14C).

Internal anatomy: Oral tube short and thick (Fig. 14D). Pharyngeal bulb covered by oral glands that form a large mass. The pharyngeal retractor muscles insert dorsally onto the bulb. The thick pharynx is variable in this species. It can arise dorsally or posteriorly to the bulb before it turns, narrows, and passes through the central nerve ring (Fig. 14E). The thin esophagus inserts into the digestive gland.

Reproductive system: The reproductive system (Fig. 14F) has an oval ampulla. Prostate tubular and folded. The spherical bursa copulatrix is smaller than the ampulla. From the bursa copulatrix emerges a thick duct connecting to the ovate receptaculum seminis.

Remarks

According to Brunckhorst (1993), the genus *Phyllidiella* Bergh, 1869 is characterized by having black and pink dorsums, with single, compound, or coalesced tubercles. Tubercles never have yellow apices (Fahrner and Beck 2000). The rhinophores are predominantly black or bicolored (black and pink). Rhinotubercles absent. The foot sole is white to grey, without distinctive markings, and the oral tentacles are separate. Internally, *Phyllidiella* has a huge mass of oral glands that overlies the pharyngeal bulb. The long pharynx is broad and thick and it leaves the pharyngeal bulb posteriorly. The esophagus is narrow and leads into the digestive gland; there is no distinct stomach region. All these characteristics are present in our specimens justifying inclusion in the genus *Phyllidiella*.

Phyllidiella has characteristic differences in its morphology and anatomy when compared to other genera (Brunck-

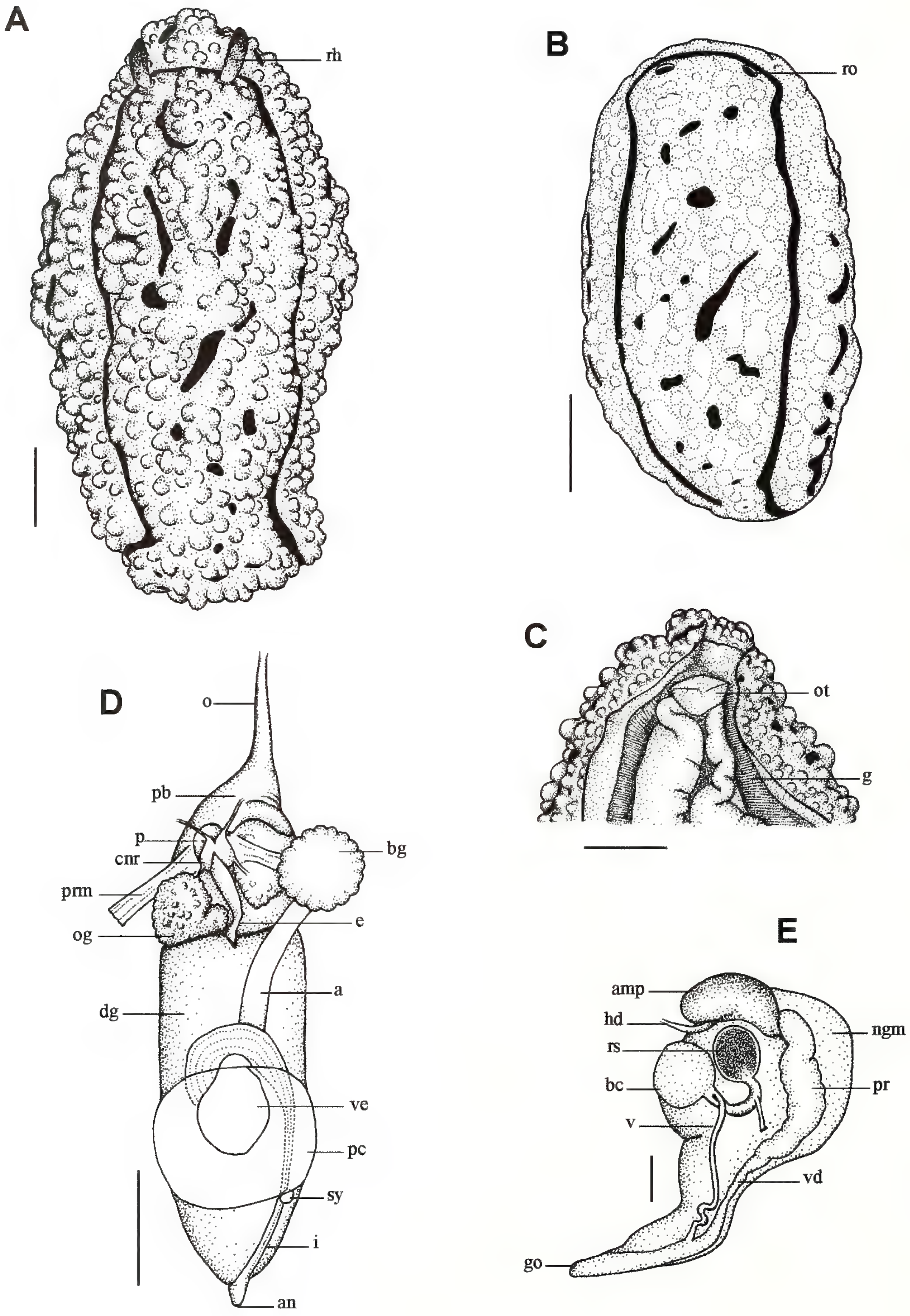
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Figure 13, *Phyllidiella hageni*. A, Drawing of the dorsal view of a preserved specimen 38.1 mm long. B, Drawing of the dorsal view of a preserved specimen 24.9 mm long. C, Drawing of the ventral view of the anterior end (the same preserved specimen illustrated in Fig. 13A). D, Diagram of the internal anatomy (the same preserved specimen illustrated in Fig. 13A). E, Diagram of the dorsal view of the reproductive system (the same preserved specimen illustrated in Fig. 13A). Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; g, gills; go, genital opening; hd, hermaphrodite duct; i, intestine; ngm, nidamental gland mass; o, oral tube; og, oral gland; ot, oral tentacle; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; prm, pharyngeal retractor muscle; rh, rhinophore; ro, rhinophoral opening; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 5 mm (A, B, C, D), 1 mm (E).

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horst 1993). The genus *Phyllidia* Cuvier, 1797 possesses large notal tubercles, mostly with yellow apices (Fahrner and Beck 2000), cream to golden-yellow rhinophores, and rhinotubercles. Internally, there are firm oral glands which often protrude posteriorly and ventrally from the pharyngeal bulb. The tubular pharynx is short and narrow. *Phyllidiopsis* Bergh, 1875 may have bicolored rhinophores, and the oral tentacles are broad and fused together. The exterior of the pharyngeal bulb appears to be quite smooth and devoid of oral glands (Gosliner and Behrens 1988, Brunckhorst 1993), but it is in fact completely enveloped by minute oral glands (Brunckhorst 1990b, 1993). The pharynx is very long and the esophagus broadens into a swollen muscular segment. The esophagus turns in a "U" before inserting into the digestive gland mass. At the base of the "U" a retractor muscle arises (Bergh 1875, 1889, Gosliner and Behrens 1988, Brunckhorst 1990a, 1990b, 1993). Members of the genus *Ceratophyllidia* Eliot, 1903 possess stalked papillae on the dorsum and partially fused oral tentacles (Brunckhorst 1993, Fahrner and Beck 2000). Individuals have two large oral glands, a long pharynx, and a long esophagus with a glandular segment (Brunckhorst 1993). The genus *Reticulidia* Brunckhorst, 1990 has smooth reticulate ridges on the dorsum (tubercles are absent), and glandular discs within the pharyngeal bulb.

The distinctive features of *Phyllidiella backeljaui* n. sp. include a pink dorsal surface with two longitudinal black bands connected by a transverse black line. The margins possess transverse black lines and the mantle edge is black. There are complex and simple tubercles on the dorsum. The rhinophores are black. The gills are dark and some specimens have rectangular gill leaflets. The oral glands form a large mass. The pharynx is swollen where it leaves the pharyngeal bulb, either dorsally or posteriorly, and the esophagus is very thin.

The main morphological differences between this and other species of *Phyllidiella* are summarized in Table 1. This species shares superficial similarities with other species of the genus such as *Phyllidiella pustulosa*, however, *P. pustulosa* has a black background, the tubercles are arranged in clusters, and the mantle edge is pink, instead of a pink background, single, compound, or coalesced tubercles, and black mantle edge. Members of *P. backeljaui* n. sp. have smaller oral glands than those of *P. pustulosa* and they are more densely grouped. The ground color of *Phyllidiella granulata* Brunckhorst, 1993 is grey, the tubercles are single and conical, and it has three encircling irregular black bands on the dorsum (Brunckhorst 1993). But Fahrner and Beck (2000) also state that *P. granulata* can have a pinkish-grey granular dorsum with three black bands and tall, compound, white tubercles. *Phyllidiella backeljaui* n. sp. externally resembles the specimens studied by Fahrner and Beck (2000), but differs from them by having a narrow black edge and numerous transverse black lines on the margin delimiting areas occupied by irregular lines or spots. *Phyllidiella lizae* also has lines crossing over each other forming an "X" in the median area, but the mantle is pale whitish-pink instead of pink, the tubercles are simple and isolated (*P. backeljaui* has complex and simple tubercles), the edge is pale pinkish-white instead of black, and the rhinophores have three colors (black, pink and white), instead of the rhinophores being entirely black. *Phyllidiella hageni* has narrow lines between the two longitudinal lines on the median part of the dorsum, and spots or black lines on the margins, but its rhinophores are black and pink instead of being entirely black. *Phyllidiella hageni* has a very short pharynx and narrower esophagus than does *P. backeljaui*. The esophagus is clearly longer than the pharynx (*P. backeljaui* has an esophagus and pharynx of similar lengths). *Phyllidiella meandrina* Pruvot-Fol, 1957 is different from *P. backeljaui* because it has tubercles forming ridges, blacks rings, and does not possess transverse black lines on the dorsum. *Phyllidiella annulata* (Gray, 1853) also has black rhinophores and black edge, but is distinct from *P. backeljaui* because the tubercles form rings and the background color of dorsum is black. *Phyllidiella cooraburrana* Brunckhorst, 1993 has black rhinophores and black edges, but the tubercles are multicompound (*P. backeljaui* possesses simple tubercles on the mantle margin) and extremely large (Brunckhorst 1993). *Phyllidiella nigra* (Hasselt, 1824) has a black dorsum with tall, rounded, dark pink to red tubercles with black bases, instead of a pink background and pink tubercles with paler apices. *Phyllidiella rosans* (Bergh, 1873) is distinct from *P. backeljaui* because it has numerous longitudinal pink ridges, a pink mantle edge, and black rhinophores with pink stalks instead of complex and simple tubercles on the dorsum, black margins, and entirely black

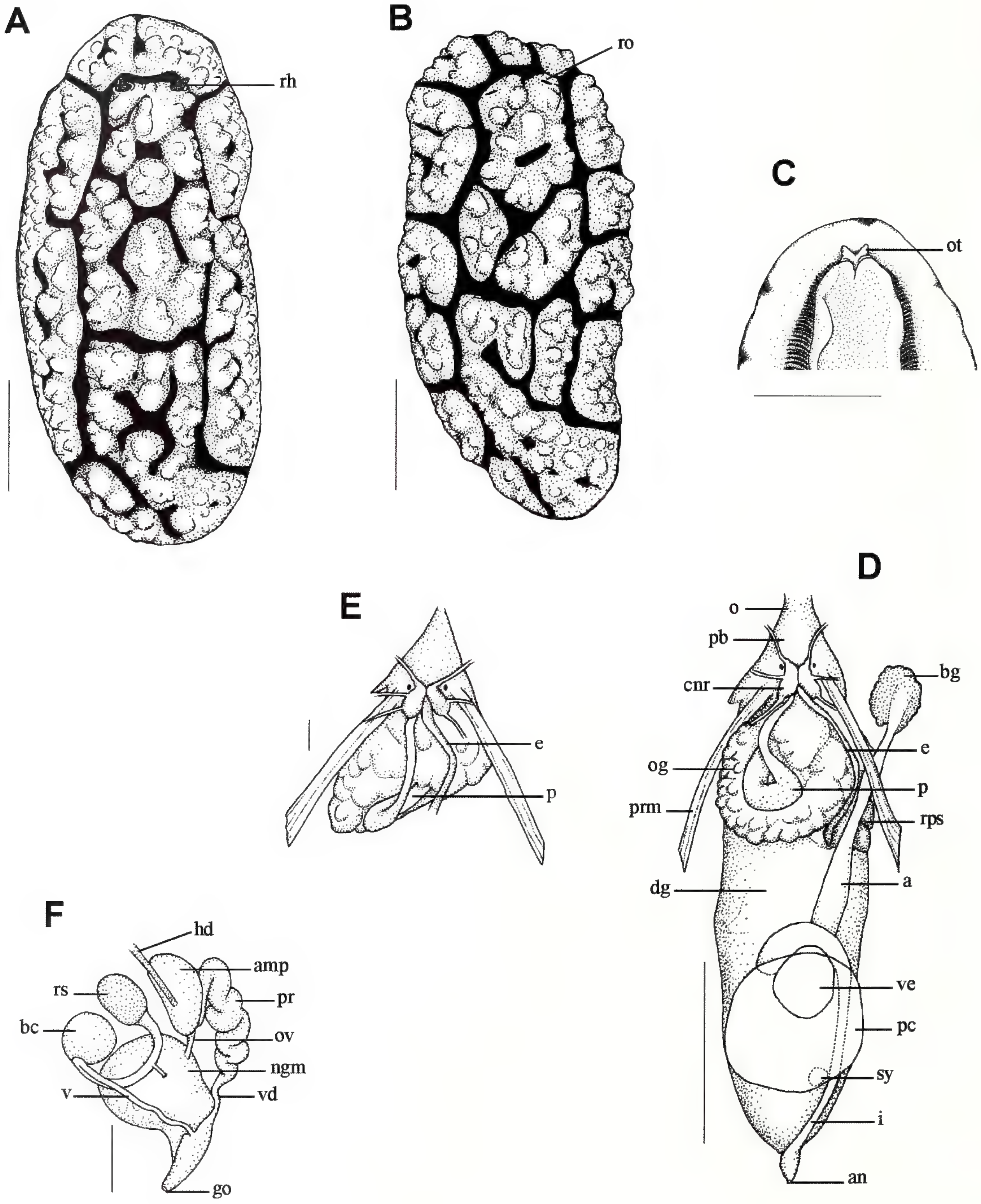
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Figure 14, *Phyllidiella backeljaui* n. sp. A, Drawing of the dorsal view of a preserved specimen 24.3 mm long, collected in Laing Island, depth 14.1 m. B, Drawing of the dorsal view of preserved specimen 22.2 mm long, collected in Laing Island, depth 14.1 m. C, Drawing of the ventral view of the anterior end (the same preserved specimen illustrated in Fig. 14A). D, Diagram of the internal anatomy (the same preserved specimen illustrated in Fig. 14A). E, Diagram of the dorsal view of the pharyngeal bulb of a specimen 23.0 mm long, collected in Laing Island, depth 0.5 m. F, Diagram of the dorsal view of the reproductive system. Abbreviations: a, aorta; amp, ampulla; an, anus; bc, bursa copulatrix; bg, blood gland; cnr, central nerve ring; dg, digestive gland; e, esophagus; go, genital opening; hd, hermaphrodite duct; i, intestine; ngm, nidamental gland mass; o, oral tube; og, oral gland; ov, oviduct; ot, oral tentacle; p, pharynx; pb, pharyngeal bulb; pc, pericardium; pr, prostate; prm, pharyngeal retractor muscle; rh, rhinophore; ro, rhinophoral opening; rps, reproductive system; rs, receptaculum seminis; sy, syrinx; v, vaginal duct; vd, vas deferens; ve, ventricle. Scale bars = 5 mm (A, B, C, D), 1 mm (E, F).

rhinophores. *Phyllidiella rudmani* has a pink dorsum and two black lines, but the lines are never connected (Fahrner and Beck 2000), the rhinophores are bicolored (black and pink), and the margin is pink. *Phyllidiella zeylanica* has a pink background, black rhinophores, and black lines on the dorsum, but it is different from *P. backeljaui* because the lines form rings, the tubercles are isolated or coalesced in rows, and the mantle edge is pink. The individuals of *P. zeylanica* we examined have a spherical ampulla, the receptaculum seminis is smaller than the bursa copulatrix, and the

Table 1. Comparison between *Phyllidiella backeljaui* n. sp. and other species of *Phyllidiella.*

	Dorsal pattern	Background color	Tubercles	Rhinophores	Mantle edge
Phyllidiella annulata	4 to 14 pink rings	Black	Small and low	Black	Black
Phyllidiella backeljaui	2 longitudinal black bands and short black lines forming "X" or a reticule and spots	Pink	Pink compound on the median	Black	Black
Phyllidiella cooraburrana	Black lines, no tubercles, forming clusters, ridges or groups	Black	Pale pink multi-compound and very large	Black	Black
Phyllidiella granulata	3 encircling irregular black bands	Grey	White compound	Black	Grey
Phyllidiella hageni	2 black longitudinal lines and short black irregular lines and spots	Pink	Coalesced, never isolated, and at the mantle margin they are single and rounded	Pink basally and black apically	Black
Phyllidiella lizae	Short lines forming an "X" medially	Pale whitish-pink	Single and isolated rarely coalesced	Black apically, pink centrally, and white basally	Pale pink to white
Phyllidiella meandrina	Black lines forming rings	Pink	Joined pink tubercles forming ridges	Black	Pink
Phyllidiella nigra	Tubercles evenly distributed (not clustered)	Black	Dark pink to red, always separated and round, very high	Black	No continuous pale edge to the mantle
Phyllidiella pustulosa	Tubercles medially arranged in clusters	Black	Pink, grouped in amalgamated clusters	Black	Pale pink
Phyllidiella rosans	Numerous longitudinal pink ridges	Black	Forming ridges	Black with pink stalks	Pink
Phyllidiella rudmani	2 black longitudinal stripes which are never connected	Pinkish white	Pinkish white, compound, arranged in longitudinal rows	Black apically with pink pale stalks	Same pale pink color as the dorsum
Phyllidiella zeylanica	Black lines forming central rings	Pale pink	Small and rounded, isolated or coalesced in rows	Entirely black	Pale pink

swollen vaginal duct is folded. *Phyllidiella backeljaui* has an ovate ampulla, the receptaculum seminis and the bursa copulatrix are of similar sizes, and the thin vaginal duct is not folded.

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Five new species of aeolid nudibranchs (Mollusca, Opisthobranchia) from the tropical eastern Pacific

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Abstract: Five new species of aeolid nudibranchs are described based on specimens collected at several localities of the tropical eastern Pacific, from Isla Isabela, Nayarit, Mexico to Parque Nacional de Coiba, Panama. Three of the new species belong to the genus *Cuthona* Alder and Hancock, 1855, one to *Eubranchus* Forbes, 1838, and one to *Cerberilla* Bergh, 1873. All are distinct from other previously known species of these genera. An additional species, possibly belonging to the genus *Herviella* Baba, 1949 is not named because of the lack of adequate anatomical information.

Key words: *Herviella*, *Cuthona*, *Cerberilla*, *Eubranchus*, Mexico, Panama

The aeolid opisthobranchs of the tropical and temperate eastern Pacific are remarkably diverse (*i.e.*, Marcus and Marcus 1967, Williams and Gosliner 1979, Gosliner 1981, Behrens 1984, 1985a, 1985b, 1987). The aeolid faunal composition of the eastern Pacific is considerably different from that of the tropical Indo-Pacific, which was reviewed in a series of regional monographs on Hawaii (Gosliner 1980), South Africa (Gosliner and Griffiths 1981), and the Indian Ocean and the south-west Pacific (Miller 1971, 1974, 2001, Rudman 1980, Schrödl 2003).

Despite the effort to collect and describe the species of the eastern Pacific, numerous species still remain undescribed, especially those of small, cryptic animals. We describe several new species of aeolid opisthobranchs collected at several localities of Mexico and Panama, contributing new information to the knowledge of this fauna.

MATERIAL AND METHODS

The material examined was collected from March 2001 to January 2005, primarily by the senior author, in several localities of the tropical eastern Pacific, including Isla Isabela (Nayarit, Mexico), Bahía de Banderas (Jalisco-Nayarit, Mexico), Manzanillo (Colima, Mexico), Ixtapa-Zihuatanejo (Guerrero, Mexico), Punta Roble and Playa Avellanas (Guanacaste, Costa Rica), and Golfo de Chiriquí, Panama, with geographic coordinates ranging from 21.5°N-105.5°W (Bahía de Banderas) to 7°N-80°W (Golfo de Chiriquí). The collecting sites included several habitats of open and protected coastlines such as coral reefs, sea grass beds, rocky reefs, estuaries, islets, islands, and seamounts.

The specimens were deposited in the Malacology Section of the Natural History Museum of Los Angeles County (LACM), the Department of Invertebrate Zoology and Geology of the California Academy of Sciences, San Francisco (CASIZ), and the invertebrate collections of the Universidad de Costa Rica—*ex.* Instituto Nacional de Biodiversidad de Costa Rica (INB). The specimens were relaxed in freezing (0°C) seawater and preserved in 90% ethanol. We dissected the specimens by making a dorsal incision from posterior to anterior. The internal features were examined and drawn using a dissecting microscope with a *camera lucida* attachment. The buccal mass was removed and placed in 10% sodium hydroxide until the radula and jaws were isolated from the surrounding tissue. The radula and jaws were then rinsed in water, dried, and mounted for examination with a scanning electron microscope (Hitachi S-3000N). Notes on the external features of the living animals were taken in the field using a dissecting microscope or a 10x magnification loupe. When possible, the specimens were photographed *in situ*; all of them were later photographed in an aquarium using a Nikon Coolpix 995 digital camera with two INON strobes; white balance set up to bright day light. The color plate was composed with Adobe Photoshop® 7.0, colors of the images were not modified.

SPECIES DESCRIPTIONS

Family Facelinidae Bergh, 1889
Genus *Herviella* Baba, 1949

Herviella sp.
(Figs. 1B, 2-3)

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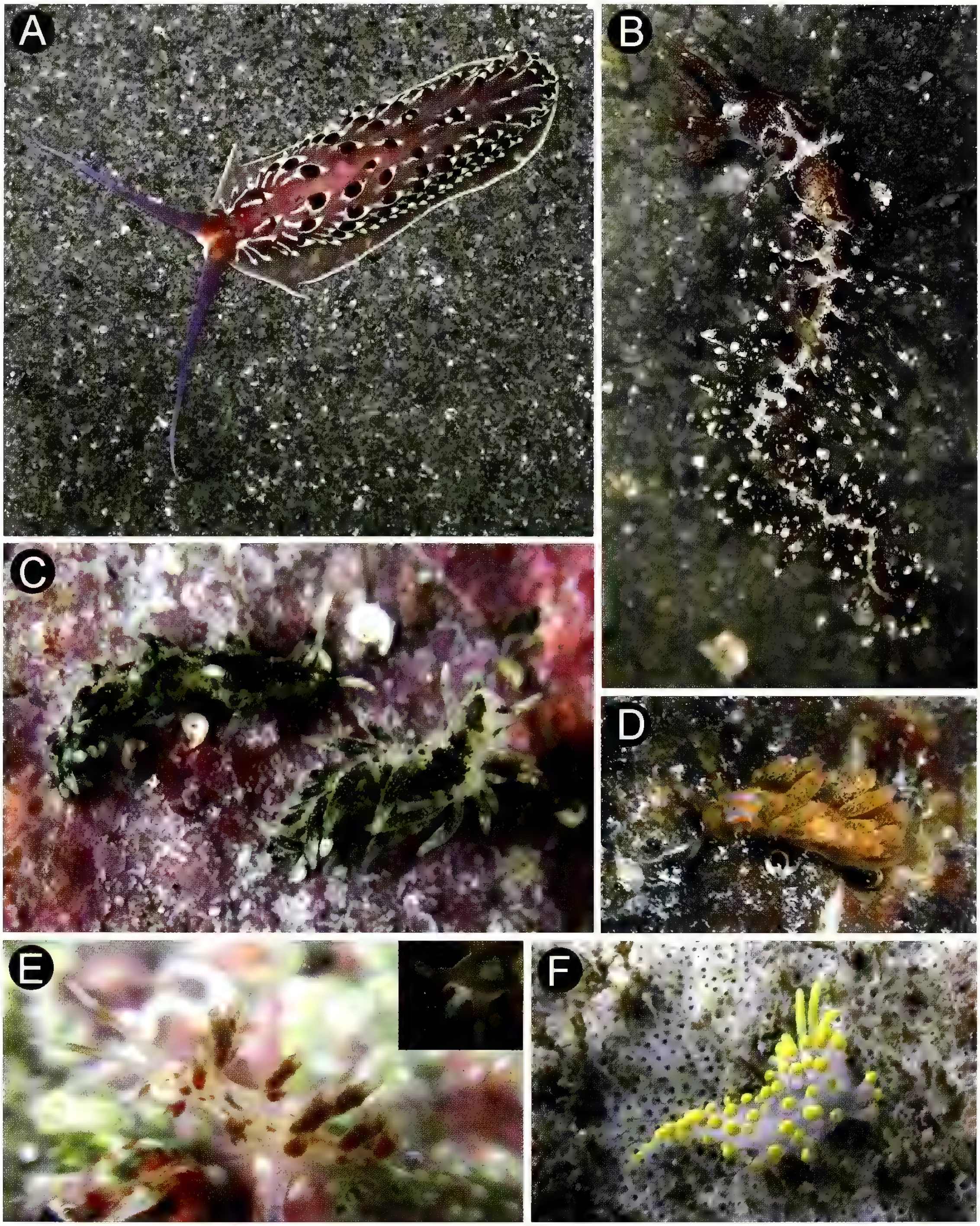

Figure 1. Photographs of eastern Pacific aeolids taken in the field. A, *Cerberilla chavezi* sp. nov., holotype, 19 mm long (LACM 3058). B, *Herviella* sp., 23 mm long (LACM 172799). C, *Cuthona destinyae* sp. nov., holotype and paratype, 6 mm long (LACM 3052, CASIZ). D, *Cuthona millenae* sp. nov., holotype, 5 mm long (LACM 3053). E, *Eubranchus yolandae* sp. nov., holotype, 6 mm long (LACM 3055), inset showing markings on cephalic region. F, *Cuthona behrensi* sp. nov., holotype, 5 mm long (LACM 3059).

Material examined

Two specimens 11 and 23 mm long, Bahía Damas (7°24.000′N, 81°39.000′W), southeast of Isla de Coiba, Parque Nacional de Coiba, Panama, 11 May 2003, collected on a floating buoy (LACM 172799).

External morphology

The body is extremely long and narrow (Fig. 1B); the larger specimen examined was 23 mm long and 4 mm wide, and the smaller specimen was 11 mm long and 3 mm wide. The pedal corners are short and rounded. There is a pair of cerata anterior to the pericardium on each side. The rest of the cerata are situated behind the pericardium and arranged in rows of one to two cerata. The larger specimen had 23 rows of cerata and the smaller one had 12. The cerata are short and slender, club-shaped, and slightly curved upwards. The rhinophores are smooth, wider at the base, and taper abruptly to a pointed tip. The oral tentacles are almost as long as the rhinophores. The gonopore is situated on the right side of the body. The position of the anus could not be determined with certainty.

The body is light brown. The dorsum bears a grayish-silver line composed of numerous minute silver specks. The line is wider at the base of the rhinophores and in the cephalic region. Posterior to the rhinophores, the line splits into two branches that surround each of the first ceratal groups and the pericardium. There is a gap in the interhepatic region where the silver line is not visible and the ground color is lighter than in the rest of the body. Posterior to the pericardium the divided silver line merges again at the center of the dorsum, branching out to each ceratal group, forming a zigzag pattern. The cerata are translucent, with the brown, non ramified projections of the digestive gland visible, and opaque white specks on the surface. The tips of the cerata are white; cnidosacs were not seen. The color of the rhinophores is translucent off-white with irregular brown blotches and occasional white specks. The oral tentacles are the same color as the rhinophores.

Internal anatomy

The radular formula is 33 × 0.1.0 in the 23 mm-long specimen. The radular teeth are two thirds as wide as long (Fig. 2A). The teeth have a smooth central projecting cusp, which is large, wide, and elongated, tapering to a rounded tip. The teeth bear from six to seven smooth denticles on each side of the cusp. The flanking denticles are about half as long as the cusp. The middle denticles on each side are slightly longer than the outermost and innermost ones. The denticles are curved inwards.

The jaws are oval in shape (Fig. 2B). There is a masticatory border consisting of a single row of seven irregular denticles (Fig. 2C). The denticles are coarse and irregular in shape, size, and position within the masticatory edge.

Reproductive system

The reproductive system is diaulic (Fig. 3A). The ampulla is an extremely wide and convoluted muscular duct that tapers abruptly distally, where it connects with the female glands. The prostate is long and narrow, coiling several times before connecting with the deferent duct. The bursa copulatrix is rounded and small. The seminal receptacle is about one-sixth of the size of the bursa copulatrix and connects directly with it. The vagina is a long and narrow duct that extends along almost the entire length of the female glands. It lacks a penial spine.

Natural history and geographic range

The specimens were found on a floating buoy that was covered with hydroids. This species is only known from the type locality in Bahía Damas, Isla de Coiba, Parque Nacional de Coiba, Pacific Coast of Panama (Hermosillo 2004).

Remarks

This species is provisionally placed in the genus *Herviella* because it possesses the following combination of characters: Elongate shape of the body with rounded pedal corners, smooth rhinophores, long oral tentacles, uniseriate radula with a protruding cusp, and few denticles and arrangement of cerata in single sloping rows. Some species of *Herviella*, including the type species, have penial spines, however, a spine is absent in *Herviella* sp., and some other species such as *Herviella africana* Edmunds, 1970 and *H. cloaca* Rudman, 1980 (Burn 1967).

We were unable to locate the position of the anus and therefore the generic placement is uncertain; for the same reason we are not naming the species until more specimens become available for study.

There are ten members of the genus *Herviella*, nine of them known from the Indo-West Pacific (Burn 1967, Rudman 1980) and one from Tanzania, eastern Atlantic (Edmunds 1970). If the generic placement is confirmed, *Herviella* sp. would be the only species of the genus that has been collected in the eastern Pacific.

Family Tergipedidae Bergh, 1889
Genus *Cuthona* Alder and Hancock, 1855

Cuthona destinyae Hermosillo and Valdés, sp. nov.
(Figs. 1C, 4-5)

Material examined

Holotype: 6 mm long, La Godornia (17°37.854′N, 101°33.562′W), Zihuatanejo, Guerrero, Mexico, 19 March 2004, collected from scrapings of the hull of the M/V *Destiny*

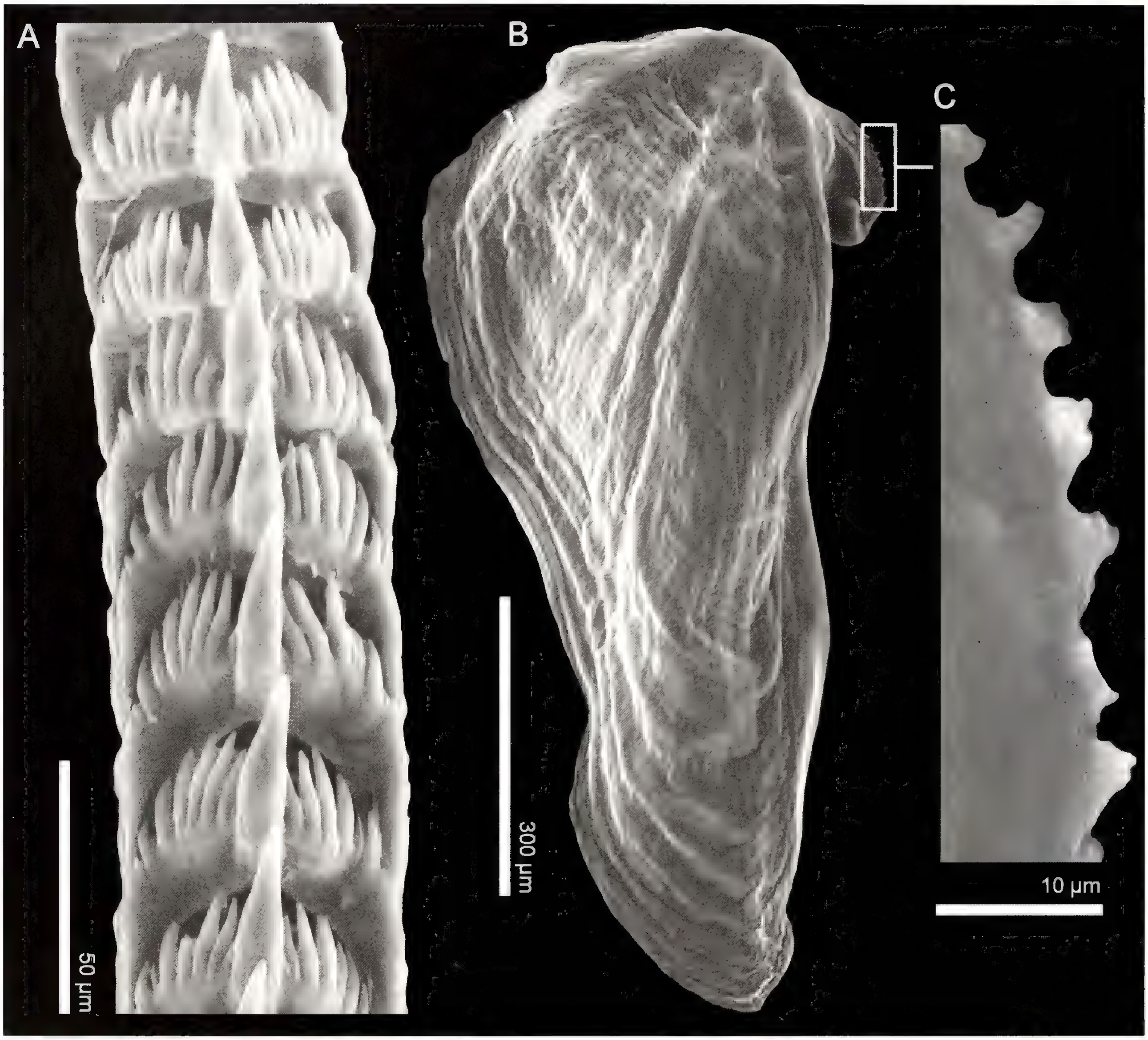

Figure 2. *Herviella* sp. (LACM 172799), scanning electron micrographs of the radula and jaw. A, Rachidian tooth, scale bar = 50 μm. B, Distal view of the right jaw, scale bar = 300 μm. C, Masticatory edge of the jaw, scale bar = 10 μm.

by A. Hermosillo and D. Behrens (LACM 3052). Paratypes: 7 specimens 6, 3, 2, 5, 4, 3, and 5 mm long, La Godornia (17°37.854′N, 101°33.562′W), Zihuatanejo, Guerrero, Mexico, 19 March 2004, collected from scrapings of the hull of the M/V *Destiny* by A. Hermosillo and D. Behrens (CASIZ). Playa Avellanas, Guanacaste, Costa Rica, (10°13.583′N, 85°50.433′W), 15 January 2001, 4 specimens, 1.5-2 mm preserved length, leg. S. Avila (INB 0003118106).

External morphology

The body is narrow and elongate. The rhinophores are smooth and long, tapering to blunt apices. The pedal corners are rounded. The genital opening is located anteriorly, below the first group of cerata. The anal opening is acleioproctic, located between the first and second rows of cerata, posterior to the pericardium at the same level as the lower-most cerata (Fig. 5A). The oral tentacles are half as long as the rhinophores, tapering to blunt tips. The cerata are lanceolate (Fig. 5C), arranged in four to five straight rows. The first row is situated anterior to the pericardium and contains four cerata; the rest of the rows contain five cerata each. The cerata located more ventrally are smaller than those located more dorsally.

The body is translucent white. There are large dark

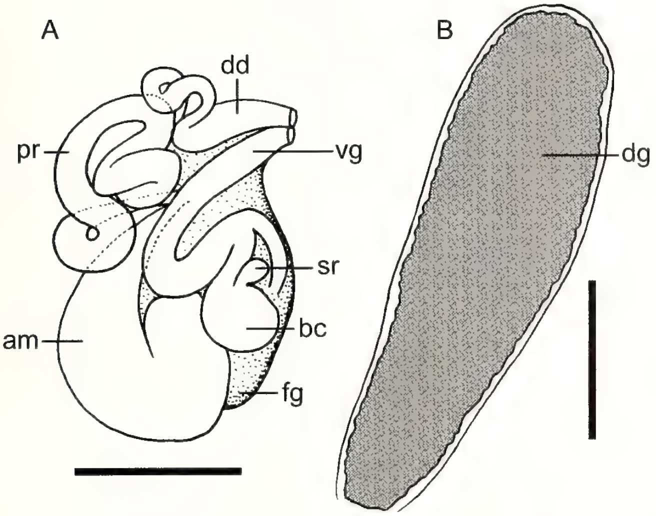

Figure 3. *Herviella* sp. (LACM 172799). A, Reproductive system, scale bar = 1 mm. B, Ceras showing the digestive gland, scale bar = 1 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; dd, deferent duct; dg, digestive gland; fg, female glands; pr, prostate; sr, seminal receptacle; vg, vagina.

patches composed of densely arranged olive-green to black spots along the midline of the notum and on the cephalic area. The sides of the body bear dark brown markings. Minute, opaque white specks are present on the lighter parts of the body. The ramifications of the digestive gland are brown. Basally, the cerata are covered with dark specks. The middle region of each ceras has a lighter band. The tip of each ceras is white, where a cnidosac can be observed. There are occasional white flecks on the surfaces of the cerata. The rhinophores have white specks on their bases, medial bands of black blotches, and white tips. The oral tentacles bear brown blotches on their sides and scattered white specks; their distal portions are lighter, with a less dense pigment present.

Internal anatomy

The radular formula is 19 × 0.1.0 in a 6 mm-long specimen. The radular teeth bear elongated, smooth central cusps (Fig. 4A). The base of the central cusp is narrow, it widens slightly distally and gradually tapers to a pointed tip. Each tooth has five to six smooth denticles on each side of the cusp, the denticles are slightly inclined inwards. The innermost denticles are shorter; they increase in length towards the outside of the ribbon. Some teeth have smaller outer denticles distal to the larger ones. The jaw is ovoid in shape (Fig. 4B). The masticatory edge of the jaw is serrated (Fig. 4C), with 31 smooth denticles; some denticles have ramified tips.

Reproductive system

The reproductive system is diaulic (Fig. 5B). The ampulla is long, convoluted and connects with the female glands. The prostate is also convoluted and long. It narrows slightly into the deferent duct. The deferent duct opens into a common atrium with an accessory penial gland. The vaginal duct is long and connects directly with the bursa copulatrix, which is rounded and small. The penis does not have a cuticular stylet.

Geographic range

This species is only known from Ixtapa-Zihuatanejo, Guerrero, Pacific coast of Mexico (Hermosillo and Behrens 2005) as *Cuthona* sp. 1 and from Costa Rica and the Galapagos Islands, Ecuador (Camacho-García *et al.* 2005) as *Cuthona* sp. 2.

Natural history: Specimens of this species were found on encrusting hydroids living on a boat hull. Numerous egg masses were collected on the same hydroids and probably belong to this species; they were white and shaped like the letter "c."

Etymology

The expedition on board of the M/V *Destiny* allowed us to learn more about the opisthobranchs of the Panamic Pacific. The specific name *destinyae* is given in appreciation to *Destiny*'s owner Steve Drogin for all his support.

Remarks

The placement of this species in *Cuthona* is based upon the presence of several diagnostic features of the genus, as discussed by Gosliner (1981), such as rounded corners of the foot; smooth, tentacular rhinophores; club-shaped cerata; acleioproctic anus; reproductive system with an accessory penial gland; and uniseriate radula.

There are 22 species of *Cuthona* known for the western hemisphere. Gosliner (1981) reported 17 valid species of *Cuthona* for the eastern Pacific and described *Cuthona phoenix* Gosliner, 1981 from La Jolla, California, which has since been reported from Guerrero, Mexico (Hermosillo and Behrens 2005) and Costa Rica (Y. Camacho-García, pers. comm.). Behrens (1985a, 1987) described two additional species: *Cuthona longi* Behrens, 1985 from the Gulf of California and *Cuthona hamanni* Behrens, 1987 from San Diego, California. Millen (1985) described *Cuthona punicea* Millen, 1985 from Vancouver, Canada. More recently, Angulo-Campillo and Valdés (2003) described *Cuthona lizae* Angulo-Campillo and Valdés, 2003 with the type locality in Baja California Sur; this species has been subsequently found in Bahía de Banderas, Jalisco-Nayarit and Isla Isabela, Nayarit, Mexico (Alicia Hermosillo, pers. obs.).

No other eastern Pacific species is similar to *Cuthona destinyae* in external coloration. Only *Cuthona phoenix* Gosliner, 1981 has a known geographic range that overlaps with

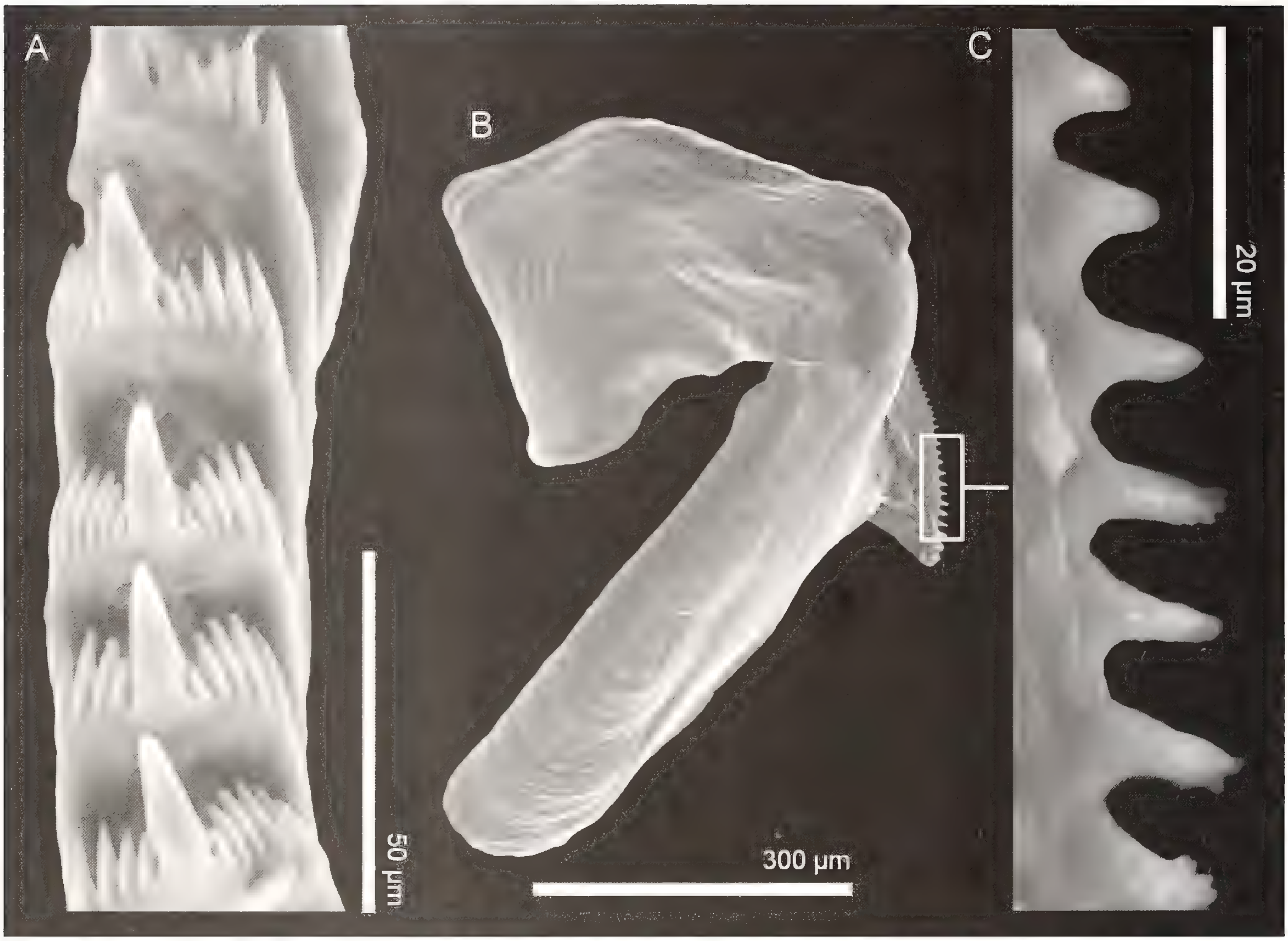

Figure 4. *Cuthona destinyae* sp. nov., holotype (LACM 3052), scanning electron micrographs of the radula and jaw. A, Radular teeth, scale bar = 50 µm. B, Distal view of the right jaw, scale bar = 300 µm. C, Masticatory edge of the jaw, scale bar = 20 µm.

that of *Cuthona destinyae* because it is known from California (Gosliner 1981) to Costa Rica (Y. Camacho-García, pers. comm.). These two species are easily distinguishable. Individuals of *C. phoenix* have only one ceras per row, whereas those of *C. destinyae* have four to five. The general body color of *C. phoenix* is translucent white with an orange tint and the cerata are orange-brown with small brown flecks (Gosliner 1981). This contrasts with the translucent white with dark blotches, central clear band, and white tip of the cerata of *C. destinyae. Cuthona phoenix* has an orange spot on the cephalic area whereas *C. destinyae* has a brownish-black spot.

Cuthona pinnifera (Baba, 1949) is known from Japan and Hawaii (Gosliner 1980) but is the only other Pacific species with a similar overall coloration to *Cuthona destinyae. Cuthona pinnifera* has a patchy dark brown coloration with some occasional opaque white spots on the dorsum. The oral tentacles are opaque white distally (Baba 1949). *Cuthona destinyae* also has brown blotches but the background color is translucent white, which gives it the appearance of a much lighter animal. The most distinctive character separating *C. destinyae* from *C. pinnifera* is the form of the rhinophores. The rhinophores of *C. pinnifera* are annulate and the rhinophores of *C. destinyae* are smooth.

Cuthona millenae Hermosillo and Valdés, sp. nov.
(Figs. 1D, 6-7)

Material examined

Holotype: 5 mm long, Los Arcos (20°32.855′N, 105°17.340′W), Bahía de Banderas, Jalisco-Nayarit, Mexico, 29 May 2003, collected under a rock at 19 m of depth (LACM 3053). Paratype: 1 specimen 5 mm long, Islas Marietas (20°42.042′N, 105°33.878′W), Bahía de Banderas, Jalisco-Nayarit, Mexico, 11 January 2005 (LACM 3050). Playa Real, NE Punta Roble, Guanacaste, Costa Rica, 20

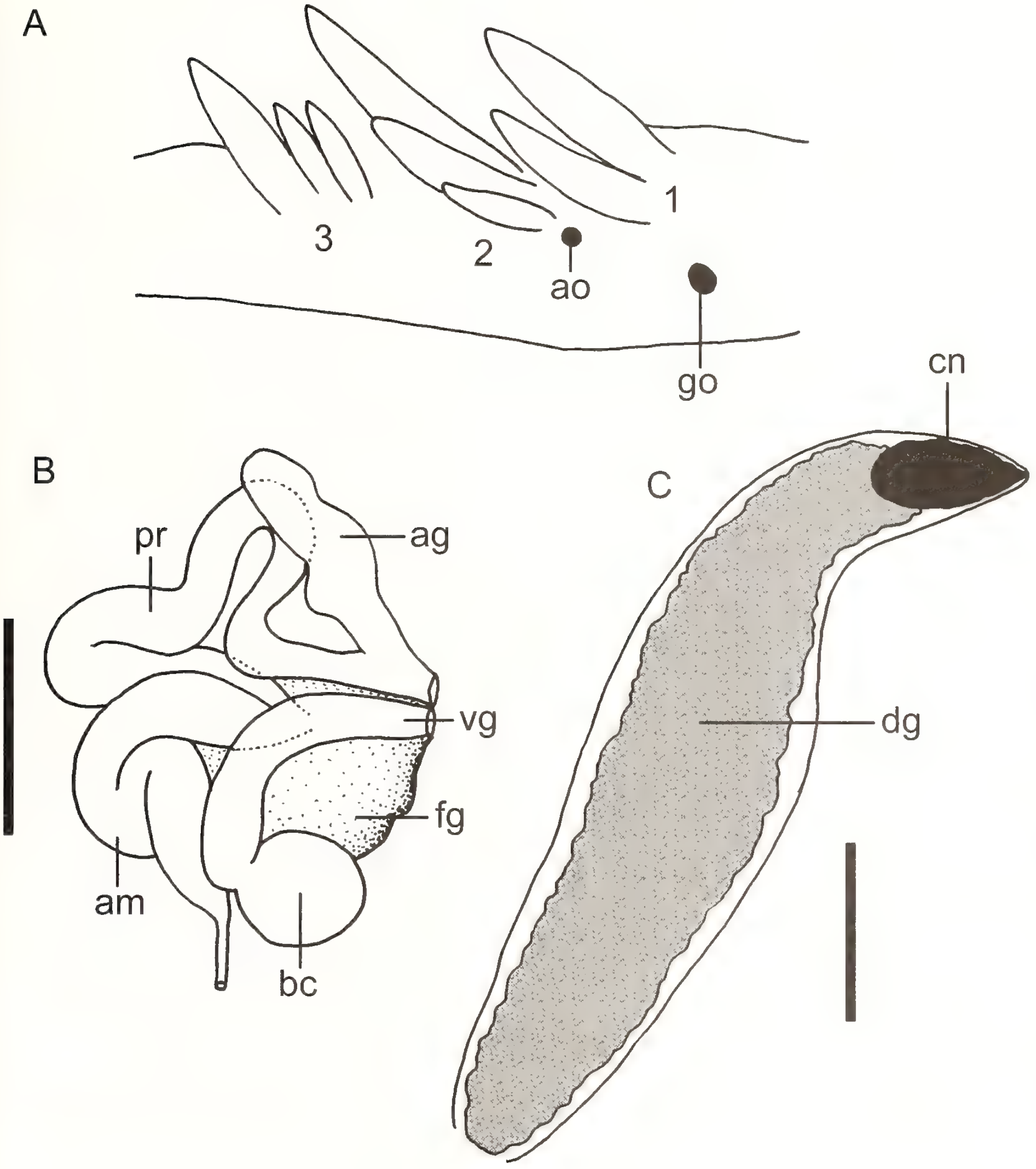

Figure 5. *Cuthona destinyae* sp. nov., holotype (LACM 3052). A, Arrangement of the anal opening and the gonopore; numbers represent the ceratal groups. B, Reproductive system, scale bar = 0.5 mm. C, Ceras, scale bar = 1 mm. Abbreviations: ag, accessory penial gland; am, ampulla; ao, anal opening; bc, bursa copulatrix; cn, cnidosac; dd, deferent duct; dg, digestive gland; fg, female glands; go, gonopore; pr, prostate; sr, seminal receptacle; vg, vagina.

April 2004 (10°23.200′N, 85°50.733′W), 5 m depth, 1 specimen 2 mm long, leg. T. M. Gosliner (INB 0003836263).

External morphology

The living animal was 5 mm in length. The body is elongated and narrow, the posterior end is long and pointed. The pedal corners are wide and rounded. The oral tentacles are about two thirds the size of the rhinophores. The rhinophores are smooth, tapering slightly to rounded tips. The cerata are relatively large compared to the size of the animal. The cerata are club-shaped with pointed apices (Fig. 7B). The cerata are arranged in two groups of straight rows. One group is located anterior to the pericardium. The first row has six cerata; the cerata become smaller ventrally. The number of cerata in the half rows posterior to the pericardium are 2(4) and 3(4). The gonopore is situated on the right side of the body.

The background color of the body is orange with darker orange and yellow spots. The cephalic portion of the body is pale whitish-blue and bears two well-defined orange lines that extend from the bases of the rhinophores to the first ceratal row. Two other orange lines are visible from the first ceras to the bases of the oral tentacles. Each rhinophore is proximally white and graduates into light yellow towards the apex, with a tan band in the middle. The oral tentacles have tan bases that extend onto the front of the cephalic area and yellow tips. The cerata are blotchy pale orange, with apical pale blue bands and bright orange pointed cnidosacs.

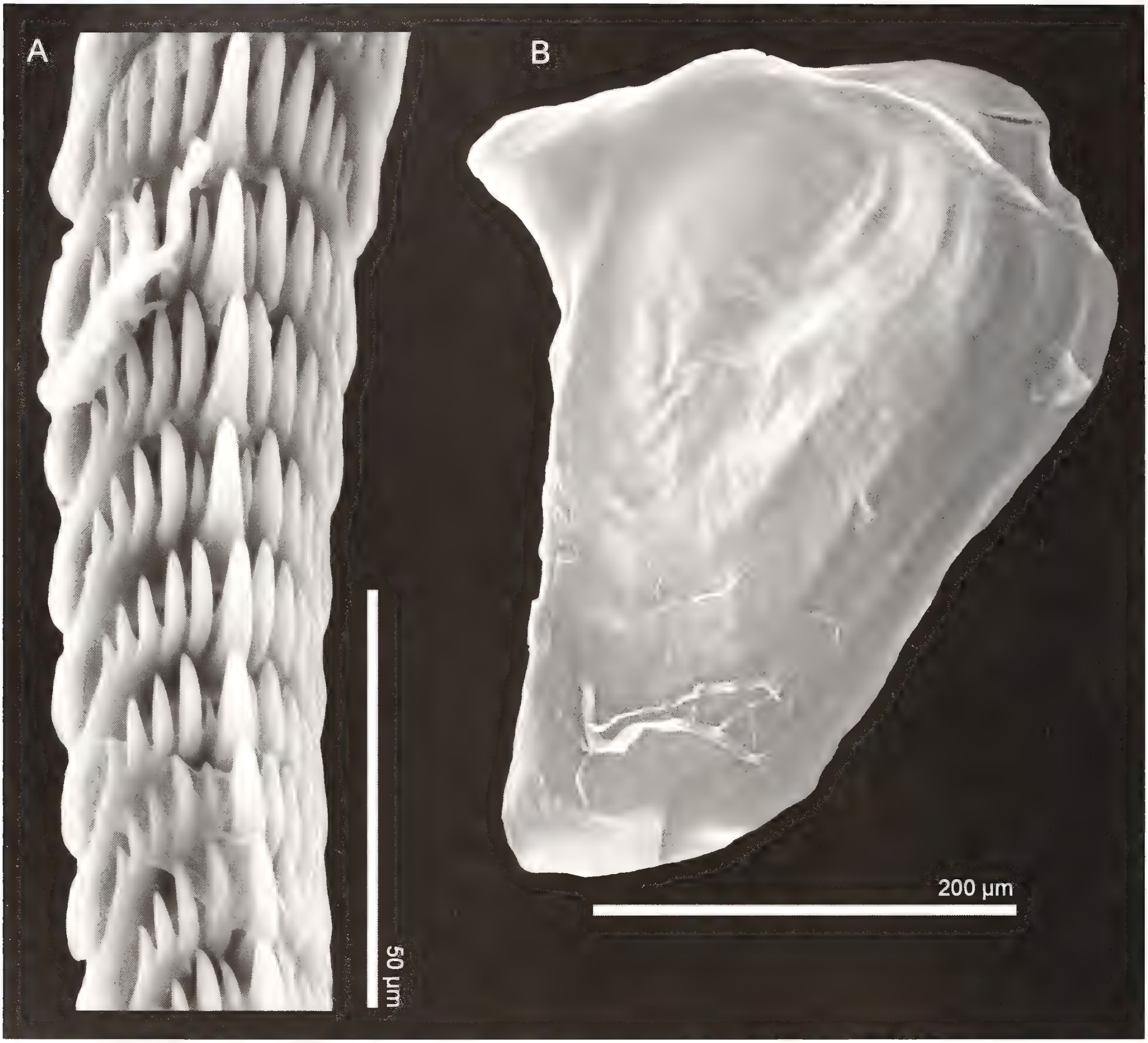

Figure 6. *Cuthona millenae* sp. nov., holotype (LACM 3053), scanning electron micrographs of the radula and jaw. A, Radular teeth, scale bar = 50 µm. B, Distal view of the left jaw, scale bar = 200 µm.

Internal anatomy

The radular formula is 42 × 0.1.0 in the holotype. The rachidian tooth bears a smooth central cusp that is just slightly longer and wider than the lateral denticles (Fig. 6A). There are four to five smooth denticles on each side of the central cusp. The outermost denticles are smaller than the ones in the middle of the row. The jaws are irregular in shape, with smooth masticatory edges (Fig. 6B).

Reproductive system

The reproductive system is diaulic (Fig. 7A). The ampulla is wide and convoluted with two folds; it narrows and connects with the female glands. The prostate is long and wide, with one fold. The prostate is about half the size of the entire reproductive system. The deferent duct is not distinguishable in dissection from the prostate. The bursa copulatrix is rounded and small and connects directly to the vaginal duct, which is the same size as the deferent duct. An accessory penial gland was not found.

Natural history and geographic range

Individuals of this species were found crawling on a

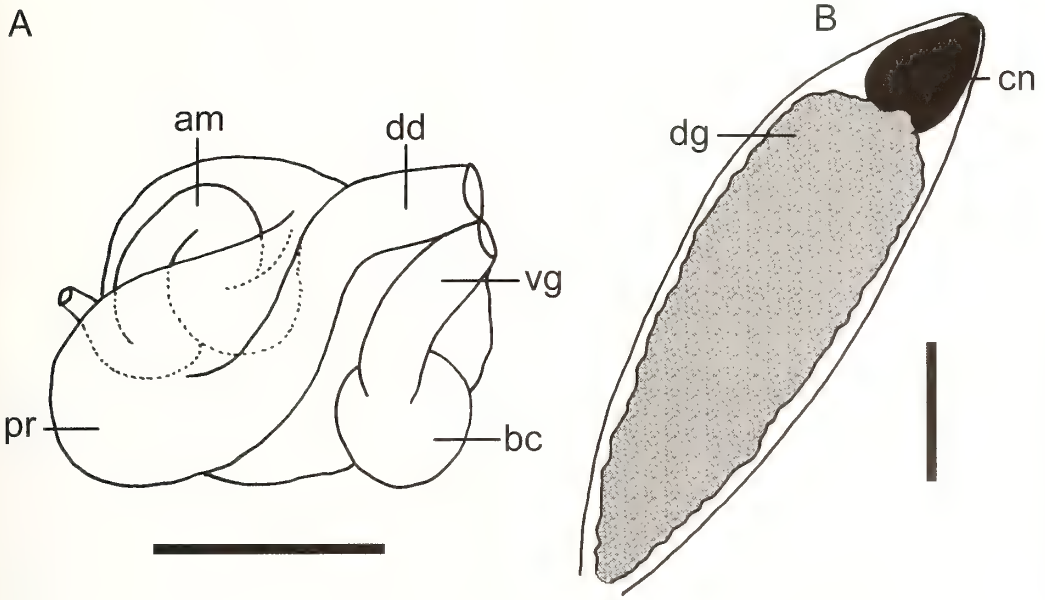

Figure 7. *Cuthona millenae* sp. nov., holotype (LACM 3053). A, Reproductive system, scale bar = 0.5 mm. B, Ceras, scale bar = 1 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; cn, cnidosac; dg, digestive gland; pr, prostate; vg, vagina.

rock wall covered by various species of hydroids. This species is only known from Bahía de Banderas, Jalisco-Nayarit, Pacific coast of Mexico (A. Hermosillo, pers. obs.) and from Costa Rica (Camacho-García *et al.* 2005), cited as *Cuthona* sp. 8.

Etymology

The specific name *millenae* is given in honor of Sandra Millen in appreciation for her contributions to the present paper and to the knowledge of the opisthobranch fauna in the eastern Pacific.

Remarks

The generic placement of *Cuthona millenae* is based on the shape of the body and the morphologies of the rhinophores and the radular teeth, which are consistent with the characteristics of other species of the genus *Cuthona* discussed by Gosliner (1981). However, an accessory penial gland was not found in *C. millenae*. This is most likely due to the small size of the specimen dissected: it was either immature or the small size of the reproductive system prevented us from observing all the organs. It is also possible that this character may be variable within the genus *Cuthona*.

Cuthona millenae is distinguishable from other members of the genus in several regards. The characteristic bright orange pigment on the tips of the cerata, the orange lines running from the bases of the rhinophores to the first ceras, and the pair of lines extending to the bases of the oral tentacles, have not been described for any other species of *Cuthona*. Only two other species of *Cuthona* are found within the geographic range of *C. millenae*: *Cuthona lizae* Angulo-Campillo and Valdés, 2003, which is known from La Paz, Baja California; Isla Isabela, Nayarit; and Bahía de Banderas, Jalisco-Nayarit; Mexico (A. Hermosillo, personal observation) and *Cuthona phoenix* Gosliner, 1981, which is known from La Jolla, California, to Guerrero, Mexico (Hermosillo and Behrens 2005) and Costa Rica (Camacho-García *et al.* 2005). The three species are readily distinguishable by their external colorations. *Cuthona lizae* has a brown body with a bright pink cephalic area and it has a large and distinctive white spot on the dorsum (Angulo-Campillo and Valdés 2003). *Cuthona phoenix* is translucent white with an orange tint but the cerata are orange-brown with small brown flecks (Gosliner 1981).

No other species described for the eastern Pacific has the combination of colors nor is as colorful as *Cuthona millenae*. Therefore, comparisons are made with other colorful species from the Indo-West Pacific. *Cuthona ornata* Baba, 1937 from Japan and *Cuthona speciosa* (Macnae, 1954) from South Africa are the species most similar to *C. millenae*. The background color of the three species is orange, but individuals of *C. millenae* are covered with opaque yellow and bright orange spots, whereas those of *C. ornata* and *C. speciosa* are solid orange (Gosliner 1981). Individuals of both *C. ornata* and *C. millenae* have colored markings on the cephalic areas, but the markings on individuals of *C. millenae* are orange and those of *C. ornata* are white. The most distinctive difference is in the color of the cerata: *Cuthona ornata* has electric blue cerata with yellow tips, *C. speciosa* has turquoise blue cerata with yellow tips, and *C. millenae* has pale yellow cerata with bright orange tips.

Cuthona diversicolor Baba, 1975 is known from Japan and Hong Kong. The background color of this species is white with yellow specks. The cerata are dark green with a white band and an orange tip (Baba 1975). The orange tips of the cerata is the only characteristic it has in common with *Cuthona millenae.* The elongated shape of *C. diversicolor* and the large number of cerata (see Baba 1975) clearly distinguish these two species.

Cuthona behrensi Hermosillo and Valdés, sp. nov.
(Figs. 1F, 8-9)

Material examined

Holotype: 5 mm long, Los Frailes Norte (7°22.370′N, 80°09.289′W), Los Frailes, Azuero Peninsula, Golfo de Chiriquí, Panama, 2 May 2003, collected under a rock at 13 m deep (LACM 3059).

External morphology

The body is elongated and narrow (Fig. 9A). The pedal corners are rounded. The foot is wider anteriorly and the posterior portion of the foot is long and thin. The rhinophores are smooth and long, with rounded apices. The diameters of the rhinophores are constant throughout their lengths. The oral tentacles are two-thirds the length of the

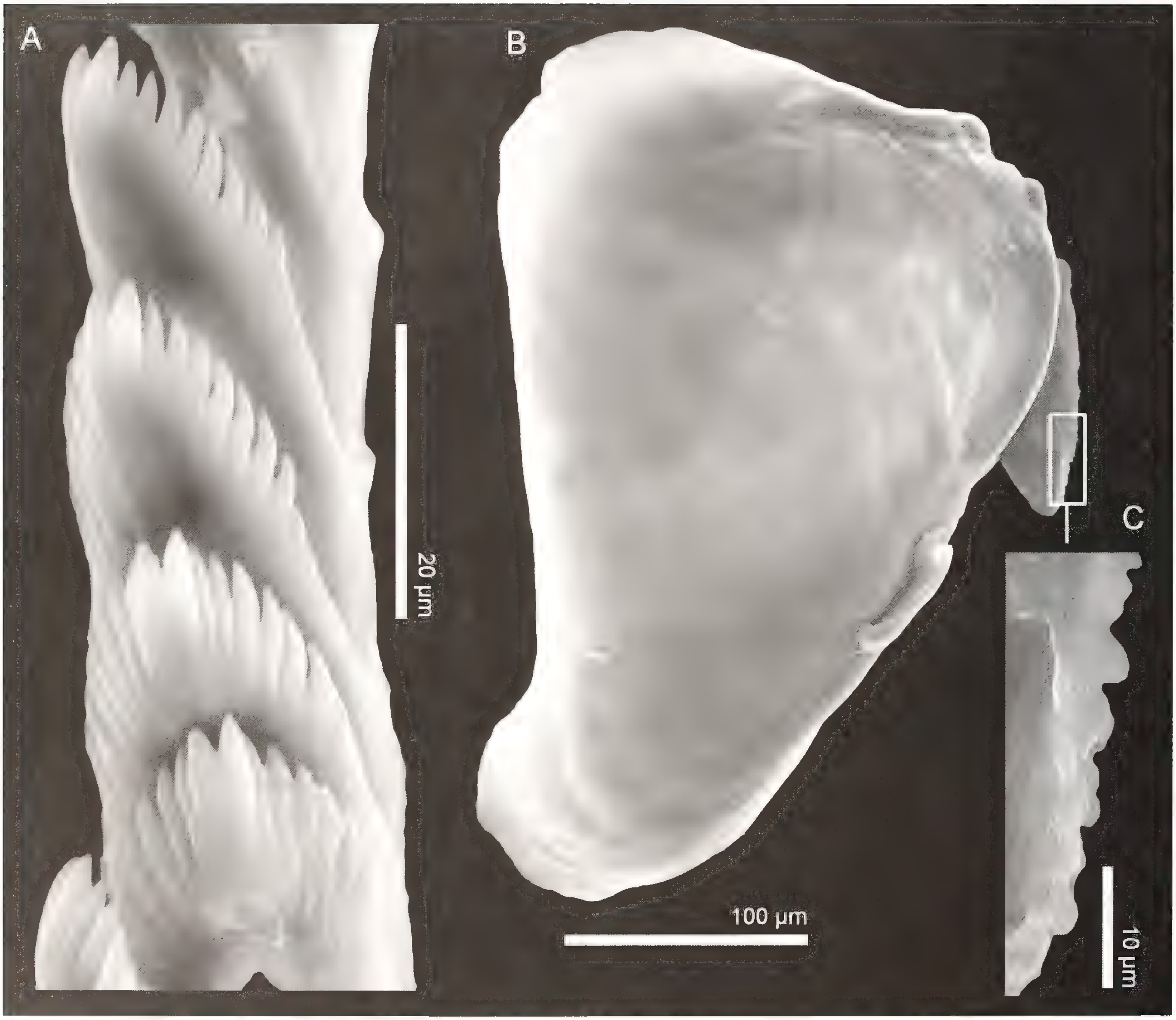

Figure 8. *Cuthona behrensi* sp. nov., holotype (LACM 3054), scanning electron micrographs of the radula and jaws. A, Radular teeth, scale bar = 20 µm. B, Distal view of the right jaw, scale bar = 100 µm. C, Masticatory edge of the jaw, scale bar = 10 µm.

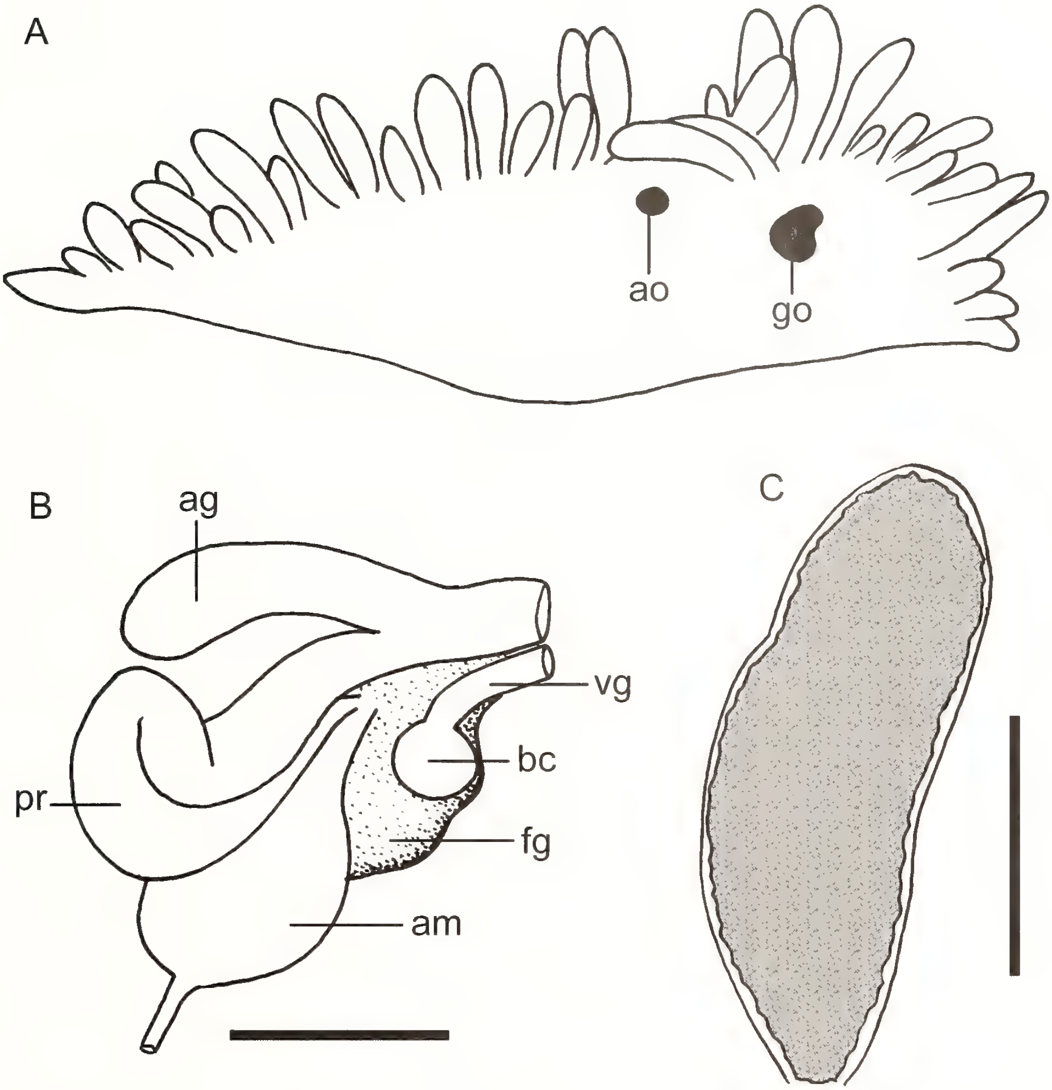

Figure 9. *Cuthona behrensi* sp. nov., holotype (LACM 3054). A, Arrangement of the anal opening and gonopore. B, Reproductive system, scale bar = 0.5 mm. C, Ceras, scale bar = 1 mm. Abbreviations: ag, accessory penial gland; am, ampulla; ao, anal opening; bc, bursa copulatrix; fg, female glands; go, gonopore; pr, prostate; vg, vagina.

rhinophores and taper slightly into rounded tips. The cerata gradually increase in width from slender bases to large, bulbous regions at the distal ends. The tips of the cerata are rounded and no cnidosacs were observed (Fig. 9C). The cerata are arranged in seven rows. The anterior rows have more cerata than do the posterior ones. The cerata closer to the center of the dorsum are larger than the more ventral ones in each row. The number of cerata in each half-row are: 1(6), 2(4), 3(3), 4(3), 5(2), 6(1), and 7 (1). The gonopore is visible on the right side, ventral to the first group of cerata. The anal opening is located anterior to the second group of cerata below the hepatic area.

The body is a translucent bright white. The rhinophores are white basally and bright yellow on the upper two thirds. The oral tentacles have the same coloration as the rhinophores. The cerata are translucent white. The ramifications of the digestive gland are opaque white with orange areas below the bright yellow rounded apices. The dorsal surface of the posterior end of the foot has a bright yellow line.

Internal anatomy

The radular formula is 17 × 0.1.0 in the holotype (Fig. 8A). The radular teeth have bifid central cusps. On each side of the cusp there are five to seven smooth, shorter denticles. The outermost denticles are smaller than the ones closer to the central cusp. The denticles are slightly curved inwards.

The jaws are oval in shape (Fig. 8B); each one has a single row of rounded, irregular denticles on the masticatory edge.

Reproductive system

The reproductive system is diaulic (Fig. 9A). The ampulla is large and pyriform. The vaginal duct is tubular, short, and connects directly with the small, round bursa copulatrix. The prostate is long and convoluted, opening into a common atrium with the accessory penial gland. Penial papillae and penial spines were not present.

Natural history and geographic range

The single specimen was found on an islet in an environment exposed to considerable wave action, under a rock covered with numerous hydroids. This species is only known only for the type locality, Los Frailes, Azuero Peninsula, Golfo de Chiriquí, Panama (Hermosillo 2004).

Etymology

The specific name is given in honor of our dear friend and colleague Dave Behrens, for his contributions to the knowledge of the opisthobranch fauna of the eastern Pacific and for his unconditional support.

Remarks

The generic placement of *Cuthona behrensi* is based on the external morphology and anatomy of this species, which fit within the diagnosis of the genus by Gosliner (1981).

Externally, *Cutona behrensi* is very different from other known species of *Cuthona*. There is no other species in this genus with only two colors that has a geographic range that overlaps the known occurrence of *C. behrensi*. Moreover, no other species of *Cuthona* is currently known from Panama.

Among the species of *Cuthona* described for the eastern Pacific, *Cuthona cocoachroma* Williams and Gosliner, 1979 also has two colors, but it has a brown-tinted white background with brown cerata; the cerata bear bright white tips (Williams and Gosliner 1979). The shape of the body is also different from that of *Cuthona behrensi*, being more slender with narrower cerata, as opposed to the stouter *C. behrensi* with inflated cerata.

Cuthona concinna (Alder and Hancock, 1843) is found in the eastern Pacific (Vancouver, Canada) and in the North Atlantic (see Behrens 1991). This species has a white background color similar to that of *Cuthona behrensi*, but it is easily distinguishable by the presence of its brown color and the more slender shape of the cerata. Moreover, the rhinophores of *C. concinna* are thick at the bases and taper abruptly into pointed apices (Behrens 1991), whereas the rhinophores of *C. behrensi* do not taper and the apices are rounded.

Cuthona divae (Er. Marcus, 1961) is known for the northern Pacific coast of the United States (see Behrens 1991). The body is white as are the rhinophores and the oral tentacles. The dark pink digestive gland can be seen through the translucent white cerata (Marcus 1961).

Family Eubranchidae Odhner, 1934
Genus *Eubranchus* Forbes, 1838

Eubranchus yolandae Hermosillo and Valdés, sp. nov.
(Figs. 1E, 10-11)

Material examined

Holotype: 6 mm long, Los Arcos (20°32.855′N, 105°17.340′W), Bahía de Banderas, Jalisco-Nayarit, Mexico, 26 May 2004, collected on a rock wall at 17 m of depth (LACM 3055). Paratypes: 2 specimens, 2-3 mm long, Los Arcos (20°32.855′N, 105°17.340′W), Bahía de Banderas, Jalisco-Nayarit, Mexico, 26 May 2004 (LACM 3056); 1 specimen, 4 mm long, Mismaloya (20°31.937′N, 105°17.700′W), Bahía de Banderas, Jalisco-Nayarit, Mexico, 21 May 2004, collected on a wall at 17 m of depth (LACM 3057).

External morphology

The shape of the body is narrow and elongated (Fig. 1E), up to 6 mm long in life. The rhinophores are smooth and very long, tapering into blunt apices. The pedal corners are rounded. The posterior portion of the foot is long and slender. The genital opening is located anterior to and below the first group of cerata. The anal opening is acleioproctic, located between the first and second rows of cerata, posterior to the pericardium and at the same level of the lower cerata. The oral tentacles are short relative to the rhinophores. The cerata located more dorsally are larger than the more ventral ones. A few cerata are much larger than the rest and are located randomly along the dorsum. The cerata are club-shaped and elongated (Fig. 11A), arranged in 7 rows of 1(3), 2(3), 3-6(2), and 7(1) cerata per half-row. There are 6 rows of cerata in the 4 mm specimen and 5 rows in the 2 and 3 mm long specimens. The first row is anterior to the pericardium. Smaller specimens readily shed the cerata when they were being collected.

The background color is translucent white. Fine opaque yellow lines can be observed along the dorsum, arranged in a random manner that varies among individuals. The sides of the body have opaque clear blue markings composed of minute specks; these marks are situated ventral to the ceratal level. The cephalic area is clear blue with two orange triangular streaks that begin anterior to the bases of the rhinophores and end at the bases of the oral tentacles. The oral tentacles are basally white, with three fourths of the length orange, and a white tip. The surface of each ceras is wine red with a distal orange band and a white cnidosac. In some

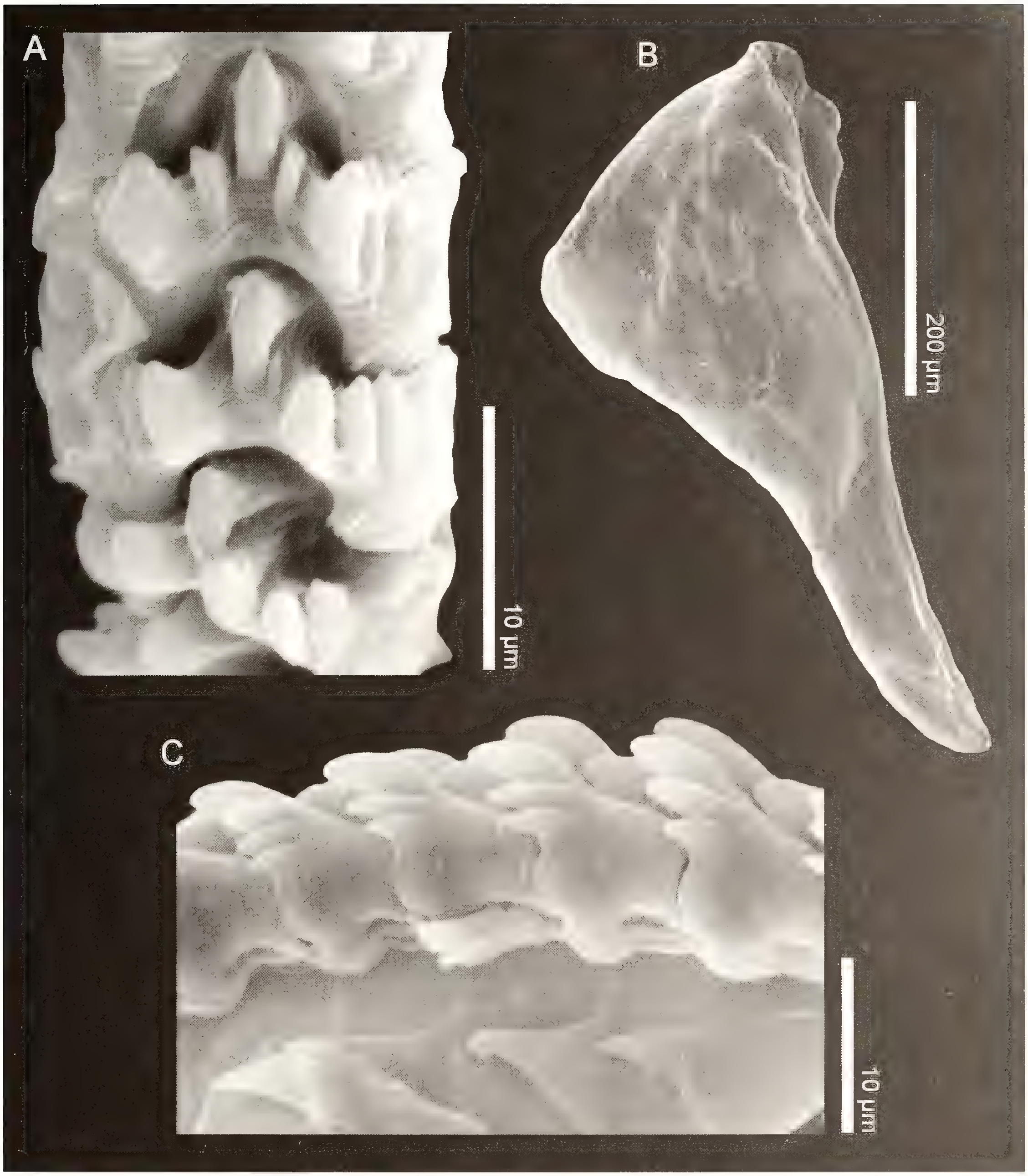

Figure 10. *Eubranchus yolandae* sp. nov., holotype (LACM 3055), scanning electron micrographs of the radula and jaw. A, Radular teeth, scale bar = 10 µm. B, Distal view of the right jaw, scale bar = 200 µm. C, Lateral view of the radular teeth, scale bar = 10 µm.

specimens the cerata are dark brown. Each rhinophore is white with a distal orange band and a lighter tip.

Internal anatomy

The radular formula is 55 × 1.1.1 in the holotype (LACM 3055). The rachidian teeth are short and wide, and have elongated, smooth central cusps (Fig. 10A). The base of the central cusp is narrower; it widens distally and gradually tapers slightly to a pointed tip. Each tooth has two to four smooth denticles on each side. There is a lateral tooth on each side of the rachidian teeth (Fig. 10C). The lateral teeth are flat, smooth, triangular plates. The jaw is composed of two elongate plates (Fig. 10B) with smooth masticatory edges.

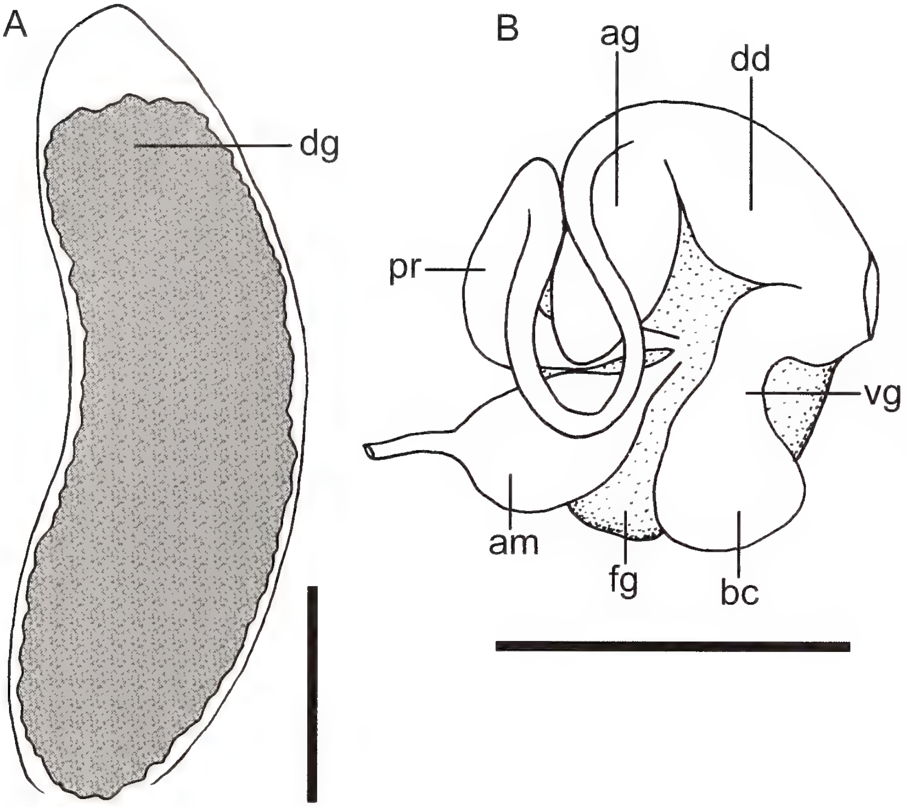

Figure 11. *Eubranchus yolandae* sp. nov., holotype (LACM 3055). A, Ceras, scale bar = 1 mm. B, Reproductive system, scale bar = 0.5 mm. Abbreviations: ag, accessory penile gland; am, ampulla; bc, bursa copulatrix; dd, deferent duct; dg, digestive gland; fg, female glands; pr, prostate; vg, vagina.

Reproductive system

The reproductive system is diaulic (Fig. 11). The ampulla is short, wide, and connects directly to the female gland. The prostate is slender, convoluted, and long, folding three times. The deferent duct is a short wide muscular duct that opens into a common atrium with the vagina. There is a large, oval accessory penial gland that opens into the proximal end of the deferent duct. The vaginal duct is short and connects directly to the bursa copulatrix, which is large and oval.

Natural history and geographic range

Eubranchus yolandae is found on rocks or macroalgae with dense hydroid coverage. Yellow, "c"-shaped egg masses were attached to the plumarid hydroids on which the nudibranchs were found; these are probably the spawn of this species. This species has been found in several localities in Bahía de Banderas, Jalisco-Nayarit, Mexico.

Etymology

The specific name is given in recognition of our colleague and friend Yolanda Camacho-García because of her contributions to the knowledge of the Panamic opisthobranch fauna.

Remarks

The generic placement of *Eubranchus yolandae* is based on the presence of a combination of features including rounded pedal corners, triseriate radula, rachidian tooth with a single cusp, lateral teeth triangular and elongated, smooth rhinophores, and club-shaped cerata (see Edmunds and Kress 1969). No other species of *Eubranchus* has a color pattern similar to *E. yolandae.* Unique to this species are the blue cephalic region with two orange bands and opaque blue markings on the sides of the body.

There are 7 species of *Eubranchus* described or reported from the eastern Pacific. Only two of those species, *Eubranchus cucullus* Behrens, 1985 and *Eubranchus madapanamensis* (Rao, 1969) are known from areas that overlap the geographic range of *Eubranchus yolandae.* Specimens of *E. cucullus* are very variable in color (Millen *et al.* 2003), therefore color cannot be used to distinguish this species. However, *E. cucullus* is clearly different from *E. yolandae* in several other regards: the former has a cowl-like cephalic region and triangular, short, oral tentacles (see Behrens 1985b), and the masticatory borders of the jaws of *E. cucullus* have over 20 denticles, whereas those of *E. yolandae* are smooth. *E. madapanamensis* is clearly distinguishable by having annulate rhinophores and highly nodular cerata, as well as the body covered with brown-red spots and the presence of bright orange apices on the cerata.

All of the other five species of *Eubranchus* from the eastern Pacific are externally very different from *Eubranchus yolandae. Eubranchus misakiensis* Baba, 1960 is known from Japan and introduced in San Francisco Bay (California); it has an off-white background color, some brown spots, brown markings, light cerata, and tentacular pedal corners. *Eubranchus olivaceus* (O'Donoghue, 1922), a possible synonym of *Eubranchus rupium* (Möller, 1842), found from Alaska to Bahía de los Angeles, Gulf of California, has a translucent white background color with irregular opaque white specks, some brown spots, and an olive green digestive gland that can be seen through the translucent cerata. *Eu-*

branchus rustyus (Er. Marcus, 1961), known from Alaska to Punta Abreojos in Baja California, has a white background with small yellow-white dots and green cerata. *Eubranchus sanjuanensis* Roller, 1872, known from Alaska to Washington, has a translucent white body, rhinophores, and oral tentacles; the cerata are bulbous, translucent with a visible bright red digestive gland, and opaque white apices. *Eubranchus steinbecki* Behrens, 1984, known from California to La Paz, Baja California Sur, has irregular and nodular cerata, and the background color is tan with dark green spots. The same coloration is present on the cephalic area, rhinophores, and oral tentacles. All these species are illustrated by Behrens (1991).

Eubranchus echizenicus Baba, 1975 from Japan is another species of *Eubranchus* that has some blue spots on the body. However, the rhinophores are red and the background color is white with red spots; the cerata are small and an opaque yellow (see Baba 1975).

Family Aeolidiidae Gray, 1827
Genus *Cerberilla* Bergh, 1873

Cerberilla chavezi Hermosillo and Valdés, sp. nov.
(Fig. 1-A, 12-13)

Material examined

Holotype: 19 mm long, La Boquita (19°06.303′N, 104°23.915′W), Bahía de Santiago, Colima, Mexico, 21 February 2004, collected at 6 m depth on a sandy bottom (LACM 3058). Paratypes: 1 specimen 11 mm long, La Cruz de Huanacaxtle (20°44.44′N, 105°23.16′W), Bahía de Banderas, Nayarit, Mexico, 14 January 2004, collected at 10 m depth at night from a sandy bottom (LACM 3059); 1 specimen 14 mm long, La Boquita (19°06.303′N, 104°23.915′W), Bahía de Santiago, Colima, Mexico, 26 March 2004, collected at 6 m depth at night on a sandy bottom (LACM 3060).

External morphology

The body is wide and elongate (Fig. 1A), up to 19 mm long in life. The anterior end of the body is broader and tapers slightly into the rounded posterior end. The foot is wider than the dorsum and has distinct tentaculiform anterior corners. The rhinophores are small, cylindrical, and smooth, and are situated near the posterior end of the cephalic region. The oral tentacles are extremely long. The cerata are arranged in ten rows, the anterior ones are more distantly separated from each other than the posterior ones. The anterior rows have fewer cerata. The cerata are club-shaped and terminate in cnidosacs at two-thirds of the length of each ceras (Fig. 13D). The cerata of the posterior rows are longer than those of the anterior ones. The center of the dorsum is devoid of cerata and is visible in the area between the anterior four rows. The longer cerata of the posterior rows cover the center of the dorsum. The number of cerata per half row are 1(5), 2(5), 3(6), and 4(7), and there are about seven cerata in rows 5-10. The gonopore is located on the right side of the body, below the cerata, between the first and second rows. The anal opening is located near the bases of the cerata, behind the pericardium, just below the fourth row of cerata. The renal opening is located anteriorly and more dorsally but close to the anal opening (Fig. 13A).

The background color is red on the center of the dorsum and translucent pinkish violet with an opaque yellow margin along the edges of the foot and pedal corners. The oral tentacles are purple. The rhinophores are red with white tips. The eyespots are visible at the bases of the rhinophores. The cerata are the same color as the body. Each has an opaque yellow line extending vertically and around the reddish-brown ramifications of the digestive gland.

Internal anatomy

The esophagus opens dorsally into the ovoid buccal mass (Fig. 13C). There is a large glandular structure (oral gland) situated near the anterior opening of the buccal mass from which two large salivary glands emerge.

The radular formula is 11 × 0.1.0 in a 14 mm long specimen (LACM 3060). The radular teeth are several times as wide as long (Fig. 12A). Each tooth has an alternating series of small and large hamate curved denticles on each side and no distinct central cusp. The center of each tooth has two small smooth denticles. The outermost denticles are slightly longer than the others and are also smooth. The jaws are composed of two wide plates with smooth masticatory edges (Fig. 12B).

Reproductive system

The reproductive system is diaulic (Fig. 13B). The hermaphroditic gland is divided into several clusters and is connected to the long and convoluted ampulla by a ramified and narrow hermaphroditic duct. The ampulla narrows and then opens into a common atrium with the vaginal duct at the point where the bursa copulatrix also connects. The prostate is long, slender, and convoluted. The prostate connects with the wide ejaculatory portion of the deferent duct that contains an oval and unarmed penis.

Natural history and geographic range

As in other members of the genus *Cerberilla*, *Cerberilla chavezi* is a burrowing species found only at night crawling on shallow sandy-muddy bottoms. When disturbed by light, the animal burrows back into the sediment, cephalic area first, positioning the oral tentacles parallel to the length of the body. The animal raises the cerata when it is physically disturbed. *C. chavezi* is known from Bahía de Banderas,

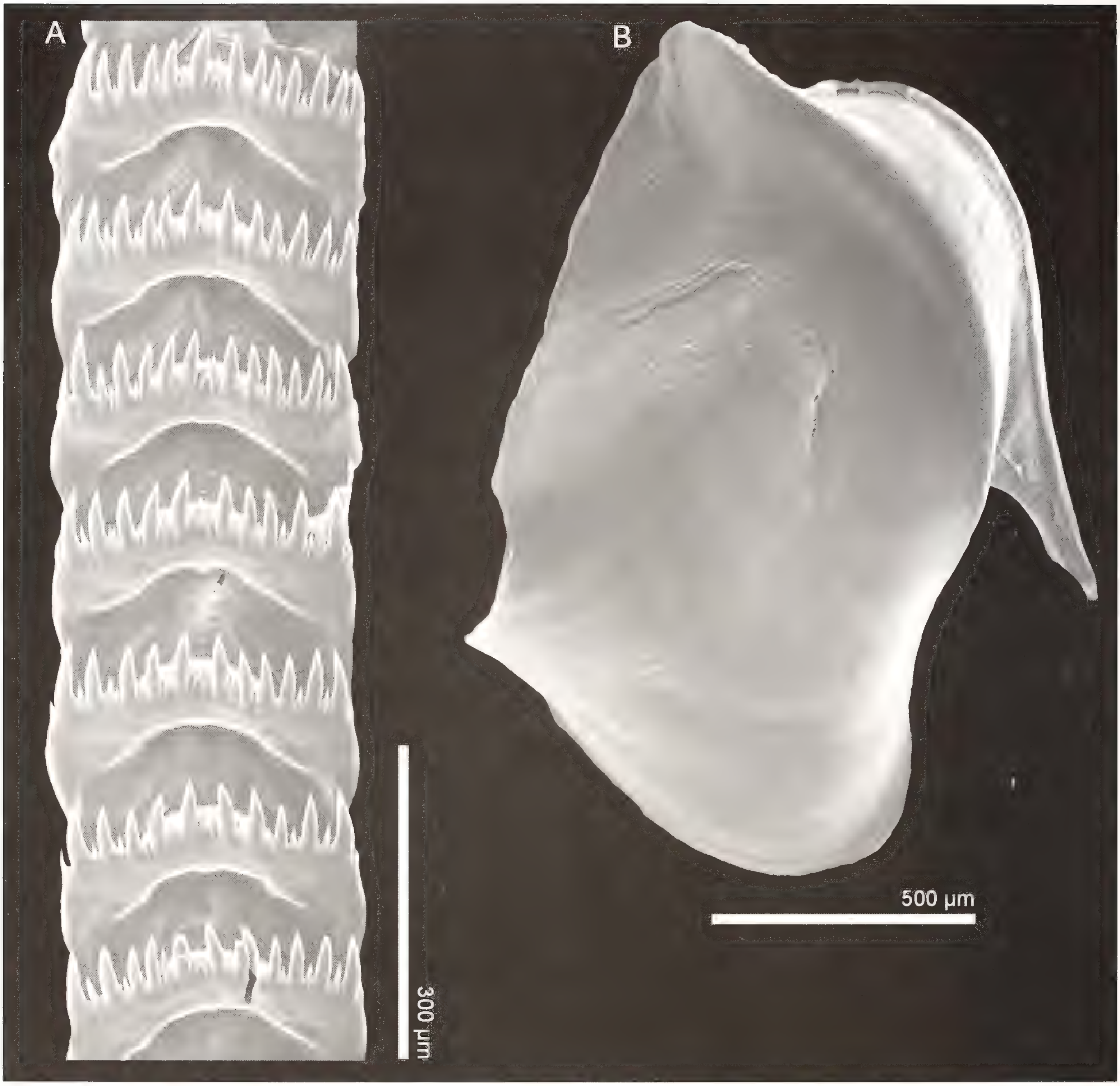

Figure 12. *Cerberilla chavezi* sp. nov., holotype (LACM 3058), scanning electron micrographs of radula and jaws. A, Radular teeth, scale bar = 300 μm. B, Distal view of the left jaw, scale bar = 500 μm.

Jalisco-Nayarit and in Bahía Santiago, Colima, Mexico (Hermosillo and Behrens 2005).

Etymology

The specific name *chavezi* is given in honor of Roberto Chavez for his invaluable assistance during the field work that produced the material examined and for his suggestion of the dive sites where *Cerberilla chavezi* was collected.

Remarks

The generic placement of *Cerberilla chavezi* is based upon the external morphology and anatomy of this species: the foot of *C. chavezi* is wider than the dorsum, with distinct,

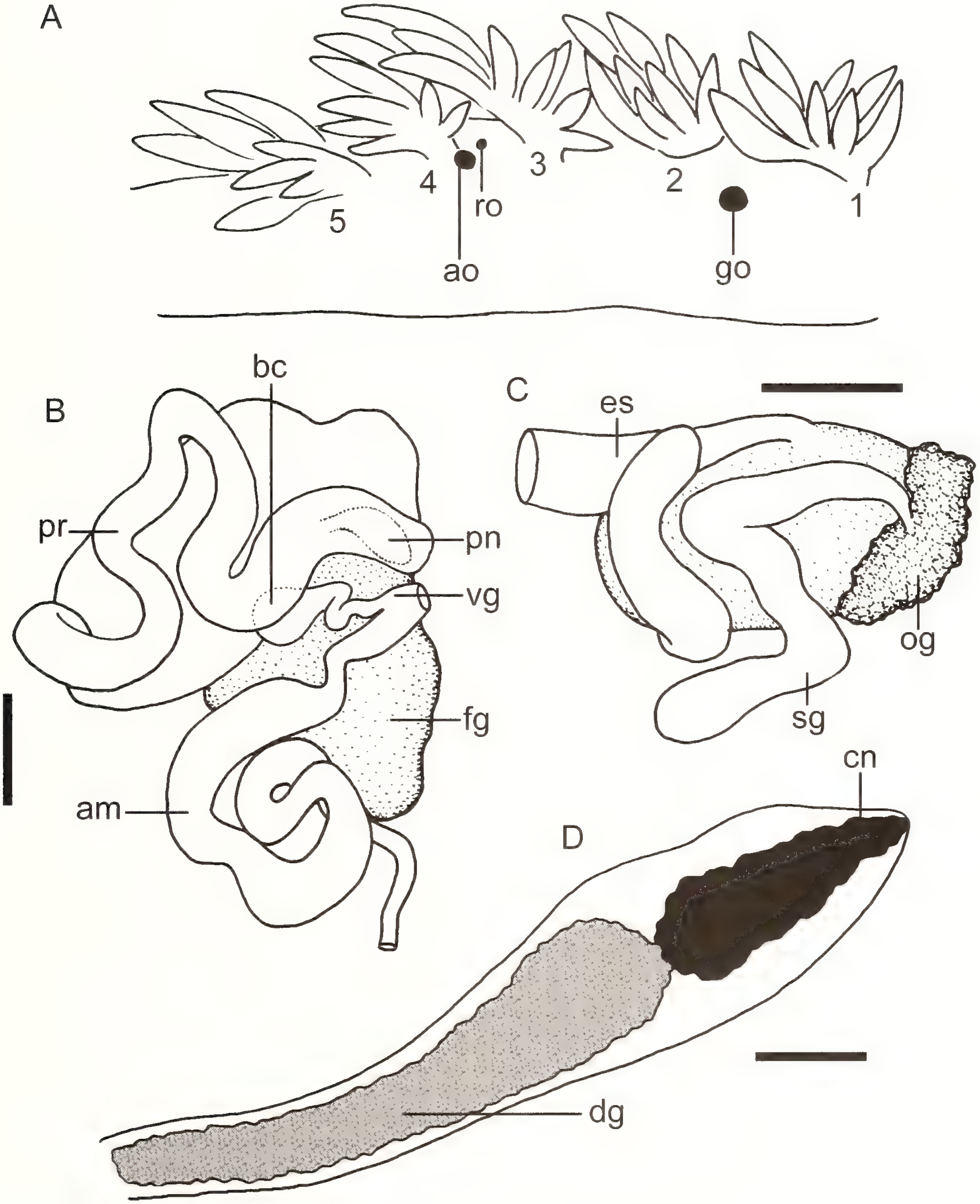

Figure 13. *Cerberilla chavezi* sp. nov., holotype (LACM 3058). A, Arrangement of the anal opening, renal opening, and gonopore; numbers represent the ceratal groups. B, Reproductive system, scale bar = 0.5 mm. C, Buccal mass, scale bar = 10 μm. D, Ceras, scale bar = 10 mm. Abbreviations: am, ampulla; ao, anal opening; bc, bursa copulatrix; cn, cnidosac; dg, digestive gland; es, esophagus; fg, female glands; go, gonopores; og, oral gland; pn, penis; pr, prostate; ro, renal opening; sg, salivary glands; vg, vagina.

very elongate pedal corners; the rhinophores are small and the oral tentacles long, the radular teeth are wide, lacking a distinct cusp and having a series of denticles all similar in size, the outermost being slightly longer. All these are diagnostic characteristics of the genus *Cerberilla* (see McDonald and Nybakken 1975).

The morphology or the radular teeth has provided the bases for identifications at the species level within *Cerberilla* (see McDonald and Nybakken 1975). However, five species of *Cerberilla* (*Cerberilla longicirrha* Bergh, 1873; *Cerberilla annulata* Quoy and Gaimard, 1832; *Cerberilla affinis* Bergh, 1888; *Cerberilla africana* Eliot, 1903; and *Cerberilla moebi* Bergh, 1888) have almost identical teeth and so are difficult to distinguish using radular characteristics alone. Therefore, other characters such as color, shape of the cerata, and anatomical features have been used instead following McDonald and Nybakken (1975). Five additional species: *Cerberilla ambonensis* Bergh, 1905; *Cerberilla tanna* Ev. Marcus and Er. Marcus, 1960; *Cerberilla asamusiensis* Baba, 1940; *Cerberilla pungoarena* Collier and Farmer, 1964; and *Cerberilla bernadettae* Tardy, 1965, have distinctive radulae, especially in the number and arrangement of the denticles (McDonald and Nybakken 1975). *Cerberilla chavezi* is another species with distinctive radular teeth with smooth, alternating, long and short denticles.

None of the previously described species of *Cerberilla* has a color pattern similar to *Cerberilla chavezi* except for *Cerberilla tanna*, described for the Gulf of Mexico. However, *C. tanna* is clearly distinguishable because the color pattern is not as bright as in *C. chavezi*, and the tips of the cerata are white, as opposed to yellow in *C. chavezi*. *C. tanna* has distinctive dark anterior markings that are absent in *C. chavezi* and the oral tentacles are whitish-orange (Marcus and Marcus 1960), whereas they are purple in *C. chavezi*. The radula of *C. tanna* is also different from that of *C. chavezi*; the outermost denticles on the teeth of *C. tanna* are at least twice as long as the rest of the denticles, which show alternation of a large denticle with two or more smaller denticles in between. In contrast, in *C. chavezi*, the radular teeth have an alternating series of a small and a large denticle on each side of the teeth and the outermost large denticles are only slightly longer than the rest of the denticles.

There are two other species of *Cerberilla* described for the eastern Pacific: *Cerberilla pungoarena* Collier and Farmer, 1964, known from the Baja Peninsula and the Gulf of California, and *Cerberilla mosslandica* McDonald and Nybakken, 1975, reported from Monterey Bay to La Jolla, California. Both species are clearly different externally from *Cerberilla chavezi*. *C. mosslandica* is white with terracotta-colored cerata; the rhinophores are white and the oral tentacles have brown and white blotches. *C. pungoarena* has a white foot and the cerata are brown with white tips; the rhinophores are also white and the oral tentacles have a pale bluish tint (Collier and Farmer 1964). There is an opaque white line on the base of each oral tentacle, and the cephalic region is markedly notched (McDonald and Nybakken 1975). The radulae of *C. mosslandica* and *C. pungoarena* are also distinct. The radula of *C. mosslandica* has 11-16 larger denticles and 17-27 smaller outermost denticles alternating with the larger ones (McDonald and Nybakken 1975). The center of the tooth has five to seven small denticles. Even the larger denticles are small compared to the size of the tooth. The outermost denticles are the same size as the rest of the large denticles. *C. pungoarena* has two long marginal denticles, the largest one is the outermost; each tooth has 10-12 small denticles, which do not alternate with larger denticles (Collier and Farmer 1964).

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The concentration of calcium carbonate in shells of freshwater snails

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Abstract: The range of concentration of calcium carbonate in the shells of various freshwater gastropods was determined using ion chromatography. Individuals of *Helisoma trivolvis* (wild) were collected from three ponds in Pennsylvania and New Jersey; individuals of *Physa* sp. were collected from one pond in New Jersey; individuals of *H. trivolvis* (Colorado strain) and *Biomphalaria glabrata* (NMRI strain) were raised in the laboratory; and individuals of *Pomacea bridgesii* were purchased commercially. The concentrations of calcium carbonate (mean % by dry weight) of the shells were as follows: *H. trivolvis* (wild), 97.0; *Physa* sp., 97.8; *H. trivolvis* (CO), 97.6; *B. glabrata*, 98.8; *P. bridgesii*, 98.2. Our data support and validate the previous claim that snail shells are comprised of 95-99.9% calcium carbonate.

Key words: Gastropoda, ion chromatography, *Biomphalaria glabrata*, *Helisoma trivolvis*, *Physa* sp., *Pomacea bridgesii*

According to Hare and Abelson (1965) and Marxen *et al.* (2003), molluscan shells consist of 95-99.9% calcium carbonate and 0.1-5% organic material by weight. However, detailed analyses of the concentration of calcium carbonate in the shells of individual species of pulmonate and prosobranch snails are for the most part not available. Some values of calcium carbonate in the shells of several pulmonates were given incidental to a study that examined the effects of parasitism by larval trematodes on the proportion of calcium carbonate in the shells of selected gastropods (White *et al.* 2005). To provide further confirmation of the 95-99.9% range of calcium carbonate reported for molluscan shells, we examined the calcium carbonate concentration of individuals from several species of field collected (wild) snails, *Helisoma trivolvis* (Say, 1816) and *Physa* sp., two species of laboratory-reared snails, *H. trivolvis* and *Biomphalaria glabrata* (Say, 1816), and one snail species purchased from a commercial supplier, *Pomacea bridgesii* (Reeve, 1856).

METHODS

Collection and maintenance of snails

Individuals of *Helisoma trivolvis* (Pennsylvania and New Jersey strain) were collected from Amwell Lake, Wildlife Management Area, East Amwell Township, Hunterdon County, New Jersey, USA (40°26′N, 74°49′W) on 15 July 2004 and from Hoch Pond, Northampton County, Pennsylvania, USA (40°47′20″N, 75°27′15″W) on 1 July 2004. Individuals of *H. trivolvis* and *Physa* sp. were collected from Delaware Pond, Knowlton Township, Columbia, New Jersey, USA (40°55′19.1″N, 75°03′49.5″W) on 1 July 2004. All wild snails were analyzed within 1-2 days of collection. A sample of water from each pond was also collected and analyzed for calcium carbonate as well.

One of us (B. Fried) has maintained a continuous culture of *Helisoma trivolvis* (Colorado strain) for more than 15 years (Fried *et al.* 1987). Stock cultures of *Biomphalaria glabrata* (NMRI strain) were obtained from Dr. Fred Lewis, Schistosomiasis Laboratory, Biomedical Research Institute, Rockville, Maryland, USA. Individuals of *Pomacea bridgesii* were purchased from Carolina Biological Supply Company (Burlington, North Carolina, USA). The specific identity of these snails was confirmed by Dr. Robert H. Cowie, University of Hawaii, Center for Conservation Research and Training, Honolulu, Hawaii, USA. Twenty individuals of *H. trivolvis* (Colorado strain), 20 of *B. glabrata*, or 2 to 3 of *P. bridgesii* were maintained at 23 ± 1°C in aerated glass jars containing 800 mL artificial spring water (ASW) as prepared by Ulmer (1970) under diffuse fluorescent light for a photoperiod of 12 h per day. The cultures were fed *ad libitum* on boiled romaine lettuce leaves, and the water was changed three times a week. Individuals of *H. trivolvis* (CO) and *B. glabrata* were maintained in the laboratory for about 6 weeks prior to use. At the time of analysis, they were sexually mature and exceeded 10 mm in shell diameter. Individuals of *P. bridgesii* were used within about 1 week of receipt from the supplier. All of the snails were negative for larval trematodes at necropsy.

Calcium carbonate determination

Ten snails were randomly selected from each population for analysis. At necropsy, snails were measured with a vernier caliper to the nearest 0.1 mm for *Helisoma trivolvis*, *Biomphalaria glabrata*, and *Physa* sp. and to the nearest 1 mm for *Pomacea bridgesii*. Measurements were taken of the maximum length of individuals of *Physa* sp. and *P. bridgesii* and of the maximum diameter of *H. trivolvis* and *B. glabrata*. The shell was dissected from the body and the body was discarded. The operculum of *P. bridgesii* was also discarded. Each sample consisted of one snail shell, which was prepared and analyzed as described in White *et al.* (2005) using a Dionex DX-120 Ion Chromatograph (Dionex, Sunnyvale, California, USA) with a Dionex AS40 automated sampler, an IonPac CG12A guard column (4 × 50 mm), an IonPac CS12A cation exchange analytical column (4 × 250 mm), and a conductivity detector. The column was eluted isocratically with 20 mM methanesulfonic acid at a flow rate of 1.0 mL/min. A Dionex cation self-regenerating suppressor ultra (100 mA) was utilized to suppress background conductivity. Standard solutions of the calcium ion were prepared at 1.00 mg/L, 5.00 mg/L, 10.0 mg/L, 25.0 mg/L, 50.0 mg/L, 100 mg/L, and 200 mg/L and used for calibration. Each sample was analyzed in triplicate with an injection volume of 25 µL and the mean concentration of calcium ion (% by dry weight) was calculated. The retention time for the calcium ion was 8.15 ± 0.50 min. Values of concentration of calcium carbonate of the test solutions were determined by PeakNet version 5.1 software as described in White *et al.* (2005). For each population, a blank was prepared in the same manner and was taken into account in calculating the final percentage of calcium carbonate of each snail shell. A single water sample from each collection site and ASW were analyzed by ion chromatography following the same procedure.

Statistical analysis

For all experiments in which multiple sample means were compared, a single factor analysis of variance (ANOVA) was used to determine whether there was a significant difference between the concentrations of calcium carbonate of the shells of various populations of snails. If a significant difference ($P < 0.05$) was found, the data were subjected to the Bonferroni method to determine among which populations the difference occurred. When two means were compared, Student's *t*-test was used to determine whether there was a significant difference ($P < 0.05$) in the calcium carbonate concentration in the shells of the two populations. SPSS version 12.0 software was used for all data analyses.

RESULTS

The percentage of calcium carbonate of the shells, the sizes of the snails used, and the concentrations of calcium carbonate of the water in which the snails were maintained are presented in Table 1. The samples from *Helisoma trivolvis* from Hoch Pond showed a significantly lower concentration of calcium carbonate than any other snail population studied (ANOVA, $P < 0.05$). Shell size could not be analyzed as a factor when looking at the concentration of calcium carbonate among all populations due to the natural size differences between species. There was no significant difference in the concentrations of calcium carbonate between the two species of laboratory-reared snails and the commercially purchased snails (ANOVA, $P > 0.05$). The shells of wild *H. trivolvis* showed no significant difference in the concentration of calcium carbonate from the laboratory-reared individuals of *H. trivolvis* (Student's *t*-test, $P > 0.05$); however, the shells of the wild population of *H. trivolvis* as a group were significantly smaller in diameter than the shells of the laboratory-reared *H. trivolvis* (Student's *t*-test, $P < 0.05$).

Table 1. Percentage of calcium carbonate by dry weight of snail shell, shell size, and calcium carbonate content (mg/L) of water.

	Species	Pond or ASW[1]	$CaCO_3$ content in shells (%) (mean ± SE)	Size of snail (mm) (mean ± SE)	$CaCO_3$ content in water (mg/L)[2]
Wild snails	*Helisoma trivolvis*[3]	Amwell Lake	97.6 ± 0.2[4]	15.0 ± 0.5[7]	141.1
	H. trivolvis[5]	Hoch Pond	95.2 ± 0.4[4]	10.4 ± 0.2[7]	39.9
	H. trivolis	Delaware Pond	98.1 ± 0.6	10.6 ± 0.3[7]	190.4
	Physa sp.[3]	Delaware Pond	97.8 ± 0.5	8.4 ± 0.1[4,6]	190.4
Laboratory-reared snails	*H. trivolvis* (CO)	ASW	97.6 ± 0.4[4]	13.2 ± 0.3[7]	32.0
	Biomphalaria glabrata[3]	ASW	98.8 ± 0.2	11.1 ± 0.3[7]	32.0
Commercially purchased snails	*Pomacea bridgesii*	ASW	98.2 ± 0.4	36 ± 2[6]	32.0

[1] ASW = artificial spring water.

[2] Water from the collection sites for wild snails and ASW for all others.

[3] From White *et al.* (2005).

[4] One sample was determined by the Q-test (90% confidence interval) to be an outlier and was excluded from the results and all statistical analyses, giving $n = 9$.

[5] This sample had a mean concentration of calcium carbonate that was significantly lower than the other samples (ANOVA, $P < 0.05$).

[6] Maximum length.

[7] Maximum diameter.

When considering only shells from the wild populations of *H. trivolvis*, the group collected from Hoch Pond had a significantly lower concentration of calcium carbonate in their shells than did the groups collected from Amwell Lake and Delaware Pond.

A correlation between the hardness of the water and the concentration of calcium carbonate in the shells was found only for the wild snails. Hoch Pond had the softest water (although still above the 20 mg/L $CaCO_3$ minimum found to limit the number of species of snails that can survive; Boycott 1936, Macan 1950). Shells of snails obtained from that pond had the lowest concentrations of calcium carbonate. Delaware Pond had the hardest water and the shells of snails collected from it had the highest concentrations of calcium carbonate. Amwell Lake had a calcium content between that of Hoch Pond and Delaware Pond. Shells of snails from that lake had concentrations of calcium carbonate between those of the snails from Hoch Pond and the snails from Delaware Pond.

The ASW had the lowest concentration of calcium carbonate, yet the shells of the laboratory-reared and commercially-purchased snails that were maintained in it had concentrations of calcium carbonate that were significantly higher than those of the wild snails (Student's *t*-test, $P<0.05$). According to the standard classification for water hardness of the U.S. Geological Survey (2006), the water from Hoch Pond and the ASW were soft, the water from Amwell Lake was hard, and the water from Delaware Pond was very hard.

DISCUSSION

In spite of considerable variation in the calcium content (mg/L) of the water in which the snails were maintained, all of the snails showed concentrations of calcium carbonate in their shells in the range of 95.2-98.8 % by weight, similar to the range reported by Hare and Abelson (1965). Thus, under conditions of variable concentrations of calcium carbonate in the water, freshwater snails are able to maintain a high concentration of calcium carbonate in their shells. No clear trend between the concentrations of calcium carbonate of the external media and the concentrations of the snail shells was found when both wild and laboratory-reared populations were considered. Freshwater snails obtain their calcium from the surrounding water and their food source (van der Borght and van Puymbroeck 1966, Young 1975), first localizing the calcium in the mantle before depositing it in the shell (Bevelander 1952). It is surprising that the laboratory-reared snails, which were raised in the softest water, had relatively high concentrations of calcium carbonate in their shells. One important difference between the laboratory-reared snails and the wild snails was that the laboratory-reared snails were fed *ad libitum*; we do not know how adequate the food supply was for the snails obtained from the wild. Individuals of *Lymnaea peregra* (Müller, 1774) and *Planorbarius corneus* (Linnaeus, 1758) reared in calcium-rich water, obtain calcium more from the water than from the food. Individuals reared in calcium-poor water, however, obtain two to four times more calcium from the food than from the water (Young 1975). This relationship between water hardness and the source of calcium may be responsible in part for the results of the present study; however, the relative role of food versus water as a source of calcium for the snails was undetermined in our study.

The data showed no direct correlation between size of the shell and concentration of calcium carbonate. Within the wild populations of *Helisoma trivolvis*, the snails from Amwell Lake were the largest; however, this did not correspond to a lower or higher concentration of calcium carbonate in the shell. The shells from the wild population of *H. trivolvis* showed no difference in concentration of calcium carbonate from those in the laboratory-reared strain, but the wild population was significantly smaller in diameter.

The data supported the claim that shells of freshwater snails are comprised of 95-99.9 % calcium carbonate by weight.

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Larval settlement and recruitment of a brackish water clam, *Corbicula japonica*, in the Kiso estuaries, central Japan

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Abstract: Population dynamics of the brackish water clam *Corbicula japonica* were examined in the Kiso estuaries (the Ibi-Nagara Estuary and the Kiso Estuary), central Japan, during the process of larval recruitment. Based on temporal variation in densities (sampling every 2 weeks for planktonic larvae, new settlers, and small individuals, sampling every month for large and commercially important individuals) from May 2001 to April 2004, we conclude that densities of large and of commercially important individuals were determined not by larval supply but by benthic processes. Density-dependent processes were detected between densities of new settlers and recruits. These processes, however, were detected for spring-summer cohorts, but not for autumn-winter cohorts. Spatial distributions of each cohort were almost the same within the Ibi-Nagara Estuary and within the Kiso Estuary, although cohorts were collected mainly in the middle to upper regions of the Ibi-Nagara Estuary but were collected in the upper region of the Kiso Estuary. A shift in an ontogenetic habitat within each cohort was detected in the Ibi-Nagara Estuary but not in the Kiso Estuary: New settlers and small individuals were collected in the upper region while large and commercially important individuals were collected in the middle region. The shift may be explained by tidal migration using byssal threads or by site-specific differences in mortality, although it was not clear why the shift was detected in the Ibi-Nagara Estuary but not in the Kiso Estuary.

Key words: population dynamics, density-dependent processes, commercially important species

The brackish water clam *Corbicula japonica* (Prime, 1864) is endemic to eastern Asia (Sakai *et al.* 1994, Harada and Nishino 1995). The clam is commonly found in estuarine waters throughout Japan except for the Ryukyu Archipelago, southern Japan, which geographically belongs to the Subtropical/Tropical Zone. The species is a target for clam fisheries in Japan, especially in the Kiso estuaries (the Ibi-Nagara and the Kiso Rivers), central Japan (see Nakamura 2000). Despite several regulations imposed to manage fisheries of *Corbicula* in Japan, the total annual catch yields of *Corbicula* species (of which approximately 99% is *C. japonica*) have decreased drastically over the last two or three decades (Mizuno *et al.* 2005), probably through the progress of eutrophication in the estuarine and coastal waters of Japan. This is true for the yields in the Kiso estuaries as well as in other areas of Japan. Traditionally in Japan, the larger hard shell clam *Meretrix lusoria* (Röding, 1798) has been commercially more important than *C. japonica*. A drastic decrease in the yield of *M. lusoria* in the Kiso estuaries occurred in the late 1970s, when the yield of *C. japonica* abruptly increased (Mizuno *et al.* 2005). This resulted in a much greater fishing effort for *C. japonica*. However, the yields of *C. japonica* in the Kiso estuaries has drastically decreased since early 1980s despite several regulations imposed on the fishery. The causes or mechanisms by which the drastic decrease in the yield of *C. japonica* in the Kiso estuaries, as well as in the other areas of Japan, may be driven are not well understood (see Nakamura 2000).

Recent studies on marine benthic invertebrates have emphasized the role of larval recruitment in the population dynamics of intertidal and subtidal organisms that have complex life cycles (those that include planktonic and benthic phases) (*e.g.*, Roughgarden *et al.* 1988, Underwood and Keough 2001), although few studies have been made in the marine environment, probably due to difficulties in identifying planktonic larvae (*e.g.*, Sakai and Sekiguchi 1992), in examining the coupling of larval transport and dispersal with oceanographic conditions (*e.g.*, Roughgarden *et al.* 1988), and in discovering larval settlement processes (*e.g.*, Connell 1985, Gaines and Roughgarden 1985, Gaines *et al.* 1985). This situation has been true also for bivalves, including the clams that are commercially important in Japan (see Miyawaki and Sekiguchi 1999, 2000, Ishii *et al.* 2001a, 2001b). Unfortunately, there is not sufficient data on larval recruitment of *Corbicula japonica*, in contrast to the clam *Ruditapes philippinarum* (Adams and Reeve, 1850), which dominates Japanese tidal flats (Miyawaki and Sekiguchi 1999, 2000, Ishii *et al.* 2001a, 2001b).

Tolerance to varying salinity by planktonic larvae and benthic stages of *Corbicula japonica* was examined in the laboratory by Tanaka (1984a, b) and Saito *et al.* (2002). Tidal transport of the larvae was investigated in relation to the salinity distribution in estuarine waters in the Kiso estuaries by Sekiguchi *et al.* (1991) and in the laboratory by Kuwabara and Saito (2003). In Lake Shinji where *C. japonica* is the most important target species for clam fisheries, growth of benthic stages of the clam was examined by Takada *et al.* (2001) and Oshima *et al.* (2004). Takada *et al.* (2001) also studied the seasonal abundance of spat of the clam, estimating the season of larval settlement. However, larval recruitment of the clam has not been studied. Nanbu *et al.* (2005) examined the spatio-temporal variations in densities of different life stages (planktonic larvae, new settlers, and small, large and commercially important individuals) of the clam in the Kiso estuaries, central Japan, to understand larval recruitment, by which benthic populations may be generated and maintained in the estuaries. In contrast to the other common and abundant bivalves (*Ruditapes philippinarum*, *Musculista senhousia* [Benson, 1842], and *Mactra veneriformis* Deshayes *in* Reeve, 1854), of which all life stages were detected around the river mouths, *C. japonica* showed a marked ontogenetic habitat shift in the Ibi-Nagara Estuary, but not in the Kiso Estuary. The primary habitat for new settlers and small individuals and of large and commercially important individuals of *C. japonica* was located in the upper and middle regions of the Ibi-Nagara Estuary, while the benthic stages were primarily found in the upper *region* of the Kiso Estuary. However, it is not clear whether the ontogenetic habitat shift is generated by migration during benthic stages or by differences in site-specific mortality of new recruits.

To understand the population dynamics of *Corbicula japonica* in the Kiso estuaries, we examined which life stage may determine the strength of catch yields (or population size) of the clam, and whether the ontogenetic habitat shift of the clam may be generated by migration during benthic stages or by differences in site-specific mortality, using the cohort separation based on three years of data (from May 2001 until April 2004) collected in the Kiso estuaries. Nanbu *et al.* (2005) examined spatio-temporal distributions of densities of each life stage of the clam, using the first two years of data from the present study.

METHODS

Study area

The Kiso Rivers (the Ibi, Nagara, and Kiso Rivers), three of the largest rivers in Japan, flow into Ise Bay on the Pacific coast of central Japan (Fig. 1). The Ibi and the Nagara Rivers join at their lower regions where both rivers are united into the Ibi-Nagara River. The Nagara River, however, has recently been closed at a point 5 km upstream by the Nagara Dam (Fig. 1). The Kiso estuaries (the Ibi-Nagara and the Kiso Estuaries), defined as the areas where bottom water has a detectable salinity of 1.0 psu, are 2-10 m in depth and have a maximal tidal range of 3 m, reaching 30 km upstream for the Ibi River and 26 km upstream (where there is a dam) for the Kiso Estuary (Japan Society of Oceanography 1985).

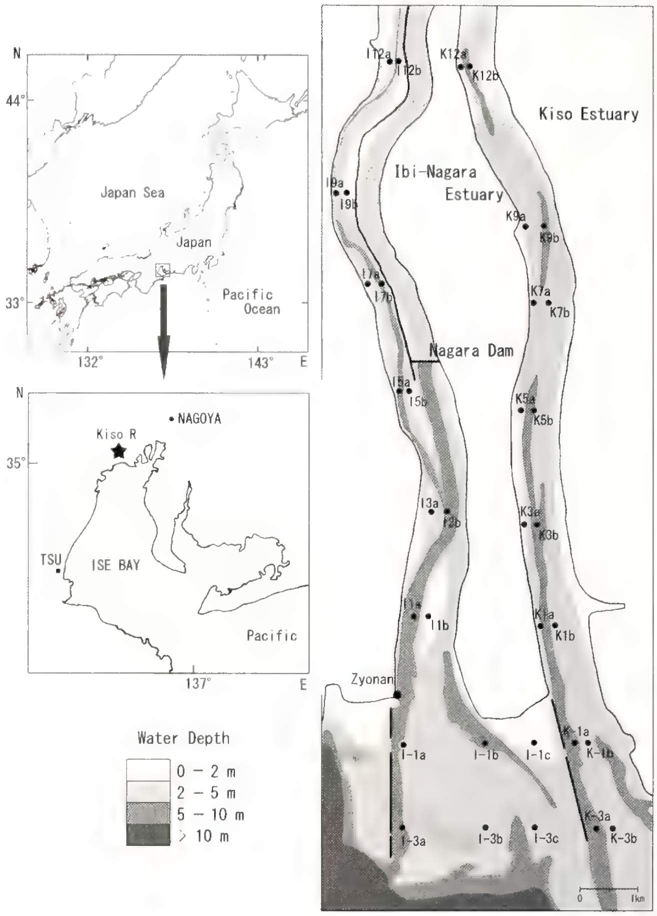

Figure 1. Study area and location of sampling stations. Solid circles, sampling stations with 2 or 3 sites (*e.g.*, I-1a, I-1b) within each sampling station; bold solid lines seaward from the estuary mouth, protection bars against the tide.

Environmental characteristics

For the last decade, the Kiso River Management Office of the Ministry of Transport and Infrastructure has continuously monitored water temperature and salinity every hour in water 0.5 m above the bottom at a site 0.5 km upstream in the Ibi-Nagara Estuary (Zyonan, see Fig. 1 for location). To examine environmental characteristics of the Kiso estuaries, we used averages over 24 h of these environmental data obtained from that office (Fig. 2A). Although we have no similar data available for the Kiso Estuary, environmental conditions are similar at the mouths of these estuaries (Mizuno *et al.* 2005).

According to Mizuno *et al.* (2005), the silt-clay fraction of sediments in the Kiso estuaries is usually less than 5.0% in dry weight, being much higher at the mouths and downstream areas of these estuaries, and lower in the upstream areas. Accordingly, bottom sediments are sandy 5 km or

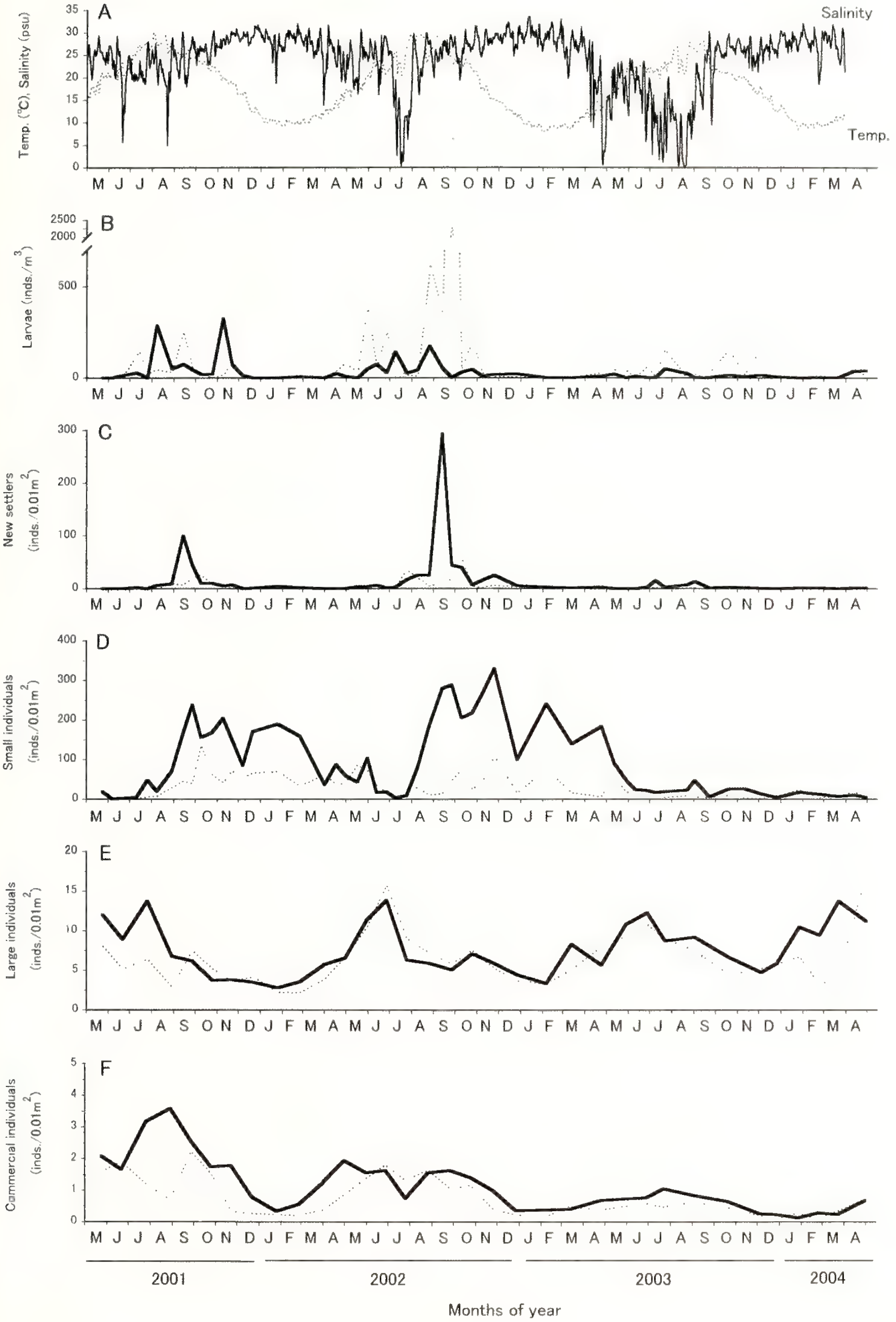

Figure 2. A, Water temperature and salinity in the Kiso estuaries, central Japan. B-F, Variation in average densities of different life stages (planktonic larvae, new settlers, small individuals, large individuals, and commercially important individuals) in the Kiso estuaries, central Japan. Solid lines, the Ibi-Nagara Estuary; dotted lines, the Kiso Estuary.

more upstream of these estuaries, although an extraordinarily high percentage (50% or more) of the silt-clay fraction occurs in the area closest to the Nagara Dam. Muddy sediment was common in troughs, so that the silt-clay fraction was very different between troughs and ridges, even at the same distance from the mouths of the estuaries.

Sampling procedures

Sampling was undertaken in the Kiso estuaries from May 2001 until April 2004. The study area, environmental characteristics, sampling procedures, and data processing were described in detail in Nanbu *et al.* (2005).

Planktonic larvae of *Corbicula japonica* were obtained at stations located 1 km seaward of each river mouth (I-1a and I-lb in the Ibi-Nagara Estuary, K-la and K-lb in the Kiso Estuary) (Fig. 1) using a vertical haul of plankton nets (22 cm in diameter, 133 um mesh openings) from the bottom to the surface every 2 weeks (except for January to March 2002). Larval density was indicated as individuals/m^3. Bivalve larvae were identified to species using a compound microscope according to Sakai and Sekiguchi (1992) and Kimura *et al.* (2004).

For sampling benthic stages of *Corbicula japonica*, 8 stations (I-3, I-1, I1, I2, I5, I7, I9, and I12 for the Ibi-Nagara Estuary, K-3, K-1, K1, K3, K5, K7, K9, and K12 for the Kiso Estuary) were located every 2 or 3 km up to 12 km upstream from the river mouth in each estuary and also 2 or 3 sites 1 km and 3 km downstream/seaward from the mouth, respectively (Fig. 1). Samples were collected at 2 or 3 sites with different depths within each sampling station area. To sample new settlers and small individuals, one sediment sample was collected with a core sampler (3.1 cm in diameter, 1.0 cm depth) from the surface layer of bottom sediments which were obtained at each site within each station using a Smith-McIntyre grab. For sampling large and commercially important individuals, one sediment sample was obtained at each site within each station using a Smith-McIntyre grab. New settlers and small individuals of the clam were collected every 2 weeks while large and commercially important individuals were collected every month. Identification of new settlers and small individuals of *C. japonica* was done following Sakai and Sekiguchi (1992) and Kimura *et al.* (2004). Density of the benthic stages of the clam was indicated as individuals/0.01m^2.

The life stages of *Corbicula japonica* were defined as in Nanbu *et al.* (2005): "Planktonic larvae" were D-shaped larvae (i.e. early-stage veligers); "new settlers" were individuals with shell lengths less than 300 μm; "small individuals" were ones with shell lengths 0.3 mm or more but less than 1.0 mm; "large individuals" were ones with shell lengths of 1.0 mm or more but less than 12.0 mm; "commercial individuals" were ones with shell lengths of 12.0 mm or more. These definitions are the same as those used to describe bivalves that are common in Japanese tidal flats *(e.g., Ruditapes philippinarum)* by Sekiguchi and his co-workers *(e.g.,* Miyawaki and Sekiguchi 1999, 2000, Ishii *et al.* 2001a, b, Nanbu *et al.* 2005) except for planktonic larvae. We defined "successful recruitment" as new settlers and small individuals that reached average shell lengths of 1.0 mm or more for each cohort.

Data analysis

Sediment samples were collected at 2 or 3 sites within each station. The density of each life stage of *C. japonica* was not significantly different between sites within each station (t-test, $p > 0.05$). We used average densities of each life stage. Based on these averages for the period from May 2001 to April 2004, we examined the differences in density of each life stage between the two estuaries and between sampling year for each estuary, using Mann-Whitney's U-test (significance level, $\alpha = 0.05$) and Kruskal-Wallis's H-test (significance level, $\alpha = 0.05$), respectively. We used Bonferroni's method ($\alpha' = 0.05$) when significant differences in density were detected between sampling years.

To separate each cohort, the shell lengths for the two groups (new settlers/small individual group, large/commercial individual group) were compiled for all stations of each estuary. However, it was difficult to separate each cohort for commercial individuals due to their small numbers. Based on these data, cohorts within each group were identified by the method of Akamine (1985), who separated polymodal length distribution into two or more normal distributions. The growth curve of each cohort was estimated based on temporal change of the mean shell length of each normal distribution.

Estimation of densities of new settlers and recruits of *Corbicula japonica*

To examine the relationships between the densities of new settlers and recruits (*i.e.*, large individuals) of the clam, using the data for cohorts that were successful in recruitment, we estimated densities of new settlers and recruits, respectively, as follows: Based on the growth curve of each successful cohort, we determined the day when average shell lengths of new settlers reached 1.0 mm. Then, assuming larval settlement day as day 0 when new settlers of each successful cohort were first collected, we fitted a regression line to the temporal change of each cohort density using a graph in which the X-axis was days after larval settlement of each successful cohort and the Y-axis was the log-transformed density of each successful cohort. Using the density data estimated for successful cohorts with a significant ($p < 0.05$) regression line, we examined the relationships between the densities of new settlers and recruits (*i.e.*, based on the data for each estuary and then for each estuary according to season), and then the relationships between the density of new settlers and the ratio of their densities (recruits/new settlers) (*i.e.*, based on the data for each estuary and then for each estuary according to season).

RESULTS

Variation in densities of different life stages of *Corbicula japonica*

The densities of planktonic larvae peaked primarily in May to December every year (Fig. 2B). There was no significant difference in larval density between the Ibi-Nagara and the Kiso Estuaries nor between sampling years for each estuary (Table 1). As seen in Fig. 2B, however, larval density in 2003 appeared to be lower than in the other years, probably due to more days with less than 10 psu in 2003 than in the other years, because salinity preferred by spawning of the clam is in the range of 9.35-21.82 psu (Asahina 1941).

Water temperature reached about 30°C in summer and decreased below 10°C in winter (Fig. 2A). On the other hand, although tending to become lower in summer and higher in winter, salinity did not indicate such a clear seasonal change but always showed irregular variations (about 15-32 psu) and occasionally marked lowering (down to <1 psu, corresponding to low larval density) owing to freshwater discharge through high rainfall in early summer. Larval densities were low or larvae were completely absent from the water column usually from December to the following April, when the water temperature decreased to below 15°C. According to laboratory rearing experiments (Kimura *et al.* 2004), larvae of the clam reared at 15°C or lower failed to settle and recruit. The larvae from earlier and later portions of a much longer period spawning of the clam every year may not contribute to generating cohorts of new settlers.

The densities of new settlers peaked primarily in July to August every year (Fig. 2C). There was no significant difference in density between the two estuaries (except for 2003) nor between sampling years for each estuary (Table 1), although the density in 2003 appeared to be lower than in the other years, possibly due to a lower larval density in 2003.

Higher densities of small individuals were found for a longer period than new settlers, occurring from August to the following April (Fig. 2D), although the density appeared to be much lower in 2003 than in the other years. In each year, density of small individuals was significantly higher in the Ibi-Nagara Estuary than in the Kiso Estuary (Table 1). The Kiso Estuary had a higher density in 2002; otherwise there was no significant difference in the density of small individuals between sampling year for each estuary (Table 1).

Variation in densities of large individuals was very similar between the two estuaries (Fig. 2E). There was no significant difference in density between these estuaries and also between sampling year for each estuary (Table 1). As seen in Fig. 2E, however, the density of large individuals appeared to be higher in 2003 than in the other years, in contrast to larvae and new settlers/small individuals (Table 1).

The density of commercially important individuals was

Table 1. Differences in densities of different life stages of *Corbicula japonica* between the Ibi-Nagara and the Kiso estuaries and between sampling years for each estuary.

2001	Ibi-Nagara	Kiso
Larvae	–	–
New settlers	–	–
Small individuals	○	×
Large individuals	–	–
Commercial individuals	○	×
2002	**Ibi-Nagara**	**Kiso**
Larvae	–	–
New settlers	–	–
Small individuals	○	×
Large individuals	–	–
Commercial individuals	–	–
2003	**Ibi-Nagara**	**Kiso**
Larvae	–	–
New settlers	○	×
Small individuals	○	×
Large individuals	–	–
Commercial individuals	–	–

Mann-Whitney's U-test (significance level, $\alpha = 0.05$).
○: significant difference with higher density.
×: significant difference with lower density.
–: no significant difference.

Ibi-Nagara	Sampling year
Larvae	2002 = 2001 = 2003 └── = ──┘
New settlers	2002 = 2001 = 2003 └── = ──┘
Small individuals	2002 = 2001 = 2003 └── = ┘
Large individuals	2003 = 2001 = 2002 └── = ──┘
Commercial individuals	2001 > 2002 > 2003 └── > ──┘
Kiso	**Sampling year**
Larvae	2002 = 2001 = 2003 └── = ─┘
New settlers	2002 = 2001 = 2003 └── = ──┘
Small individuals	2002 = 2001 = 2003 └── > ──┘
Large individuals	2003 = 2002 = 2001 └── = ──┘
Commercial individuals	2001 > 2002 > 2003 └── = ──┘

Kruskal-Wallis' H-test (significance level, $\alpha = 0.05$).
>: significant difference.
=: no significant difference.
Multiple comparison ($\alpha' = 0.05$; Bonferroni's method).

significantly lower in 2003 than in the other years (Table 1) and their density appeared to decline from 2001 to 2004 (Fig. 2F).

Cohort separation of *Corbicula japonica*

In the Ibi-Nagara Estuary, 21 cohorts of new settlers and small individuals and 16 cohorts of large individuals were identified (Fig. 3B). Of these cohorts, 7 were found to settle and to succeed in recruitment through the three-year investigation. Larval settlement for 2 cohorts (i, ii) occurred in August to September 2001. For 4 cohorts (iii-vi), the larval settlement season in 2002 varied depending on cohort: Cohorts iii, iv, and v settled in January, May to June, and September, respectively. Larval settlement for the remaining cohort occurred in April of 2003. Of these 7 cohorts, significant regression lines were fitted to the temporal change

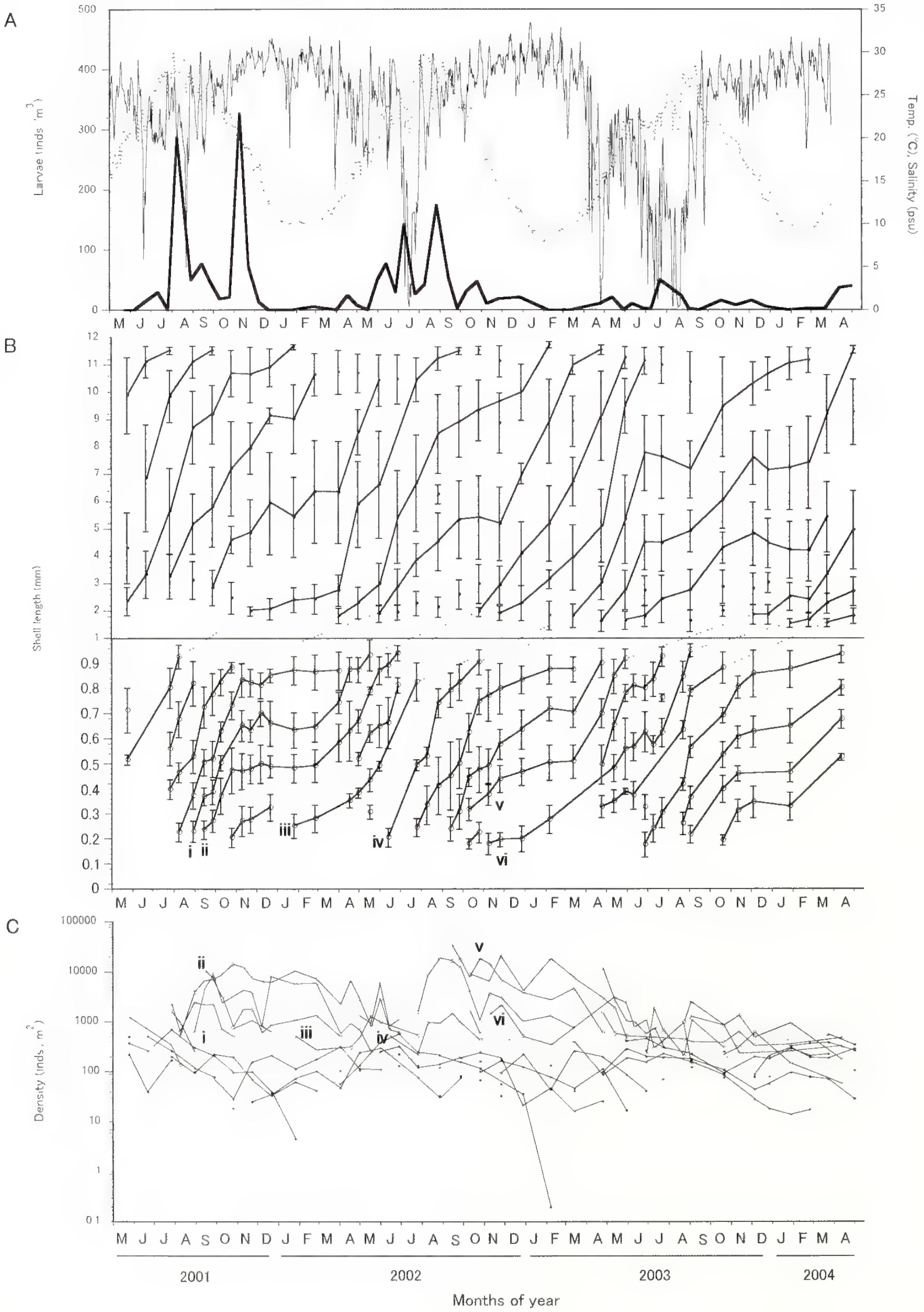

Figure 3. Cohorts of benthic stages of *Corbicula japonica* in the Ibi-Nagara Estuary, central Japan. A, Bold solid lines, larval density; thin solid lines, salinity; dotted lines, water temperature. B, i-vi, cohorts successful in recruitment; solid or open circles with vertical lines, averages of shell lengths and standard error; horizontal solid line, shell length 1.0 mm, which we defined as the size for successful recruitment. C, i-vi, cohorts same as in B.

of density from larval settlement to recruitment for 6 cohorts (cohort i-vi) (Fig. 3C). These cohorts (except cohort iii) appeared to settle in August to November.

In the Kiso Estuary, 12 cohorts of new settlers and small individuals and 13 cohorts of large individuals were identified (Fig. 4B). Of these cohorts, 7 were detected to settle and to succeed in recruitment through the three-year investigation. Larval settlement for cohorts 1 and 2 occurred in August to September 2001. For 3 cohorts (3-5), larval settlement occurred in July to September 2002. Larval settlement for the remaining 2 cohorts occurred in December 2002 and in July 2003, respectively. Significant regression lines were fitted to the temporal change of density from larval settlement to recruitment for 5 cohorts (1-5) (Fig. 4C). These cohorts appeared to settle in July to September.

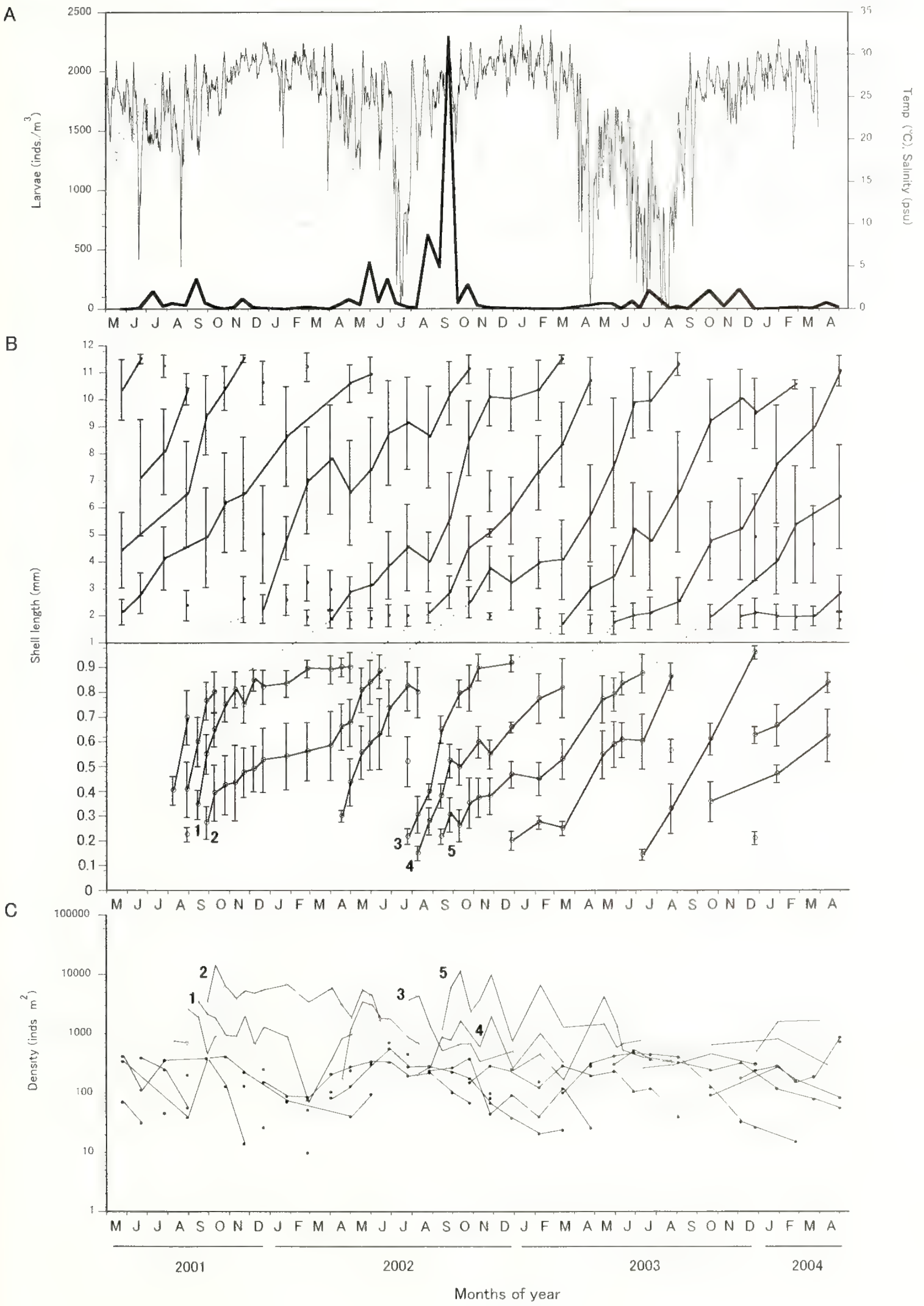

Figure 4. Cohorts of benthic stages of *Corbicula japonica* in the Kiso Estuary, central Japan. A, Bold solid solid lines, larval density; thin solid lines, salinity; dotted lines, water temperature. B, 1-5, cohorts successful in recruitment; solid or open circles with vertical lines, averages of shell lengths and standard error; horizontal solid line, shell length 1.0 mm, which we defined as the size for successful recruitment. C, 1-5, cohorts same as in B.

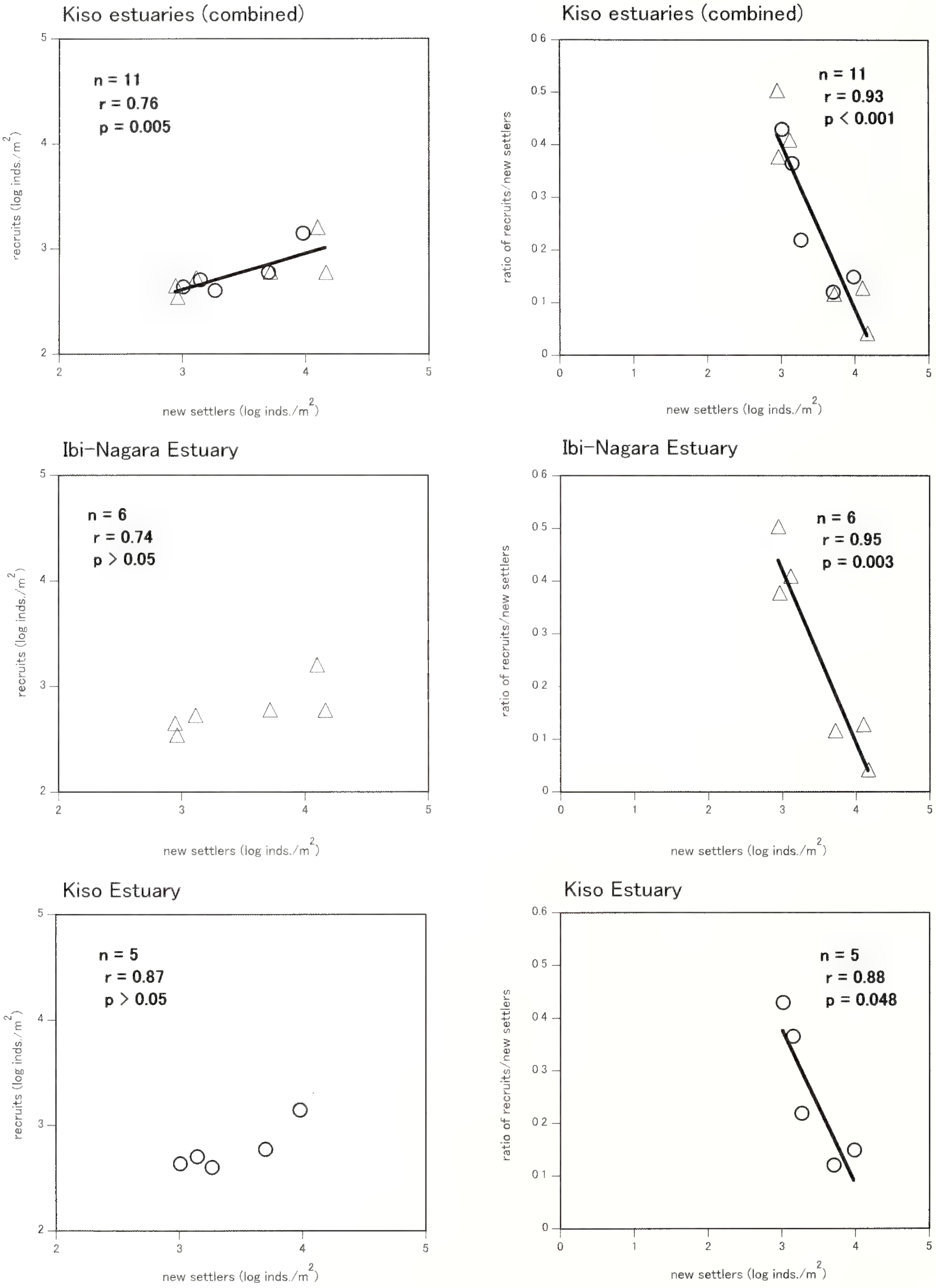

Figure 5. Relationships between densities of new settlers and recruits of *Corbicula japonica* in the Kiso estuaries, central Japan. Upper figures, data for the two estuaries combined; middle figures, data for the Ibi-Nagara Estuary; lower figures, data for the Kiso Estuary; left figures, density of new settlers *vs.* density of recruits; right figures, density of new settlers *vs.* the ratio of their densities (recruits/new settlers); open circles, data for the Ibi-Nagara Estuary; triangles, data for the Kiso Estuary; n=number of cohorts.

Based on the data for successful cohorts in the Kiso estuaries, it took nearly two years from larval settlement for individuals to reach commercially viable shell lengths. Takada *et al.* (2001) and Oshima *et al.* (2004) estimated shell growth of clams using growth rings on the shell surface and found a similar growth rate as in the present study.

As indicated in Figs. 3B and 4B, the densities of new settlers in the cohorts identified in 2003, which originated in planktonic larvae and new settlers with much lower densities, were considerably lower than in the other years (Figs. 2B, 2C). Density peaks of new settlers appeared to generate successful cohorts of benthic stages (compare Fig. 4B with Fig. 4A). However, as indicated by comparing Fig. 3B with Fig. 3A, peaks of densities of planktonic larvae did not always contribute to the generation of successful cohorts of benthic stages. The larvae from earlier and later periods of spawning of the clam every year may not contribute to generating cohorts of new settlers.

Relationships between densities of new settlers and recruits of *Corbicula japonica*

Based on the data from 11 successful cohorts (6 from

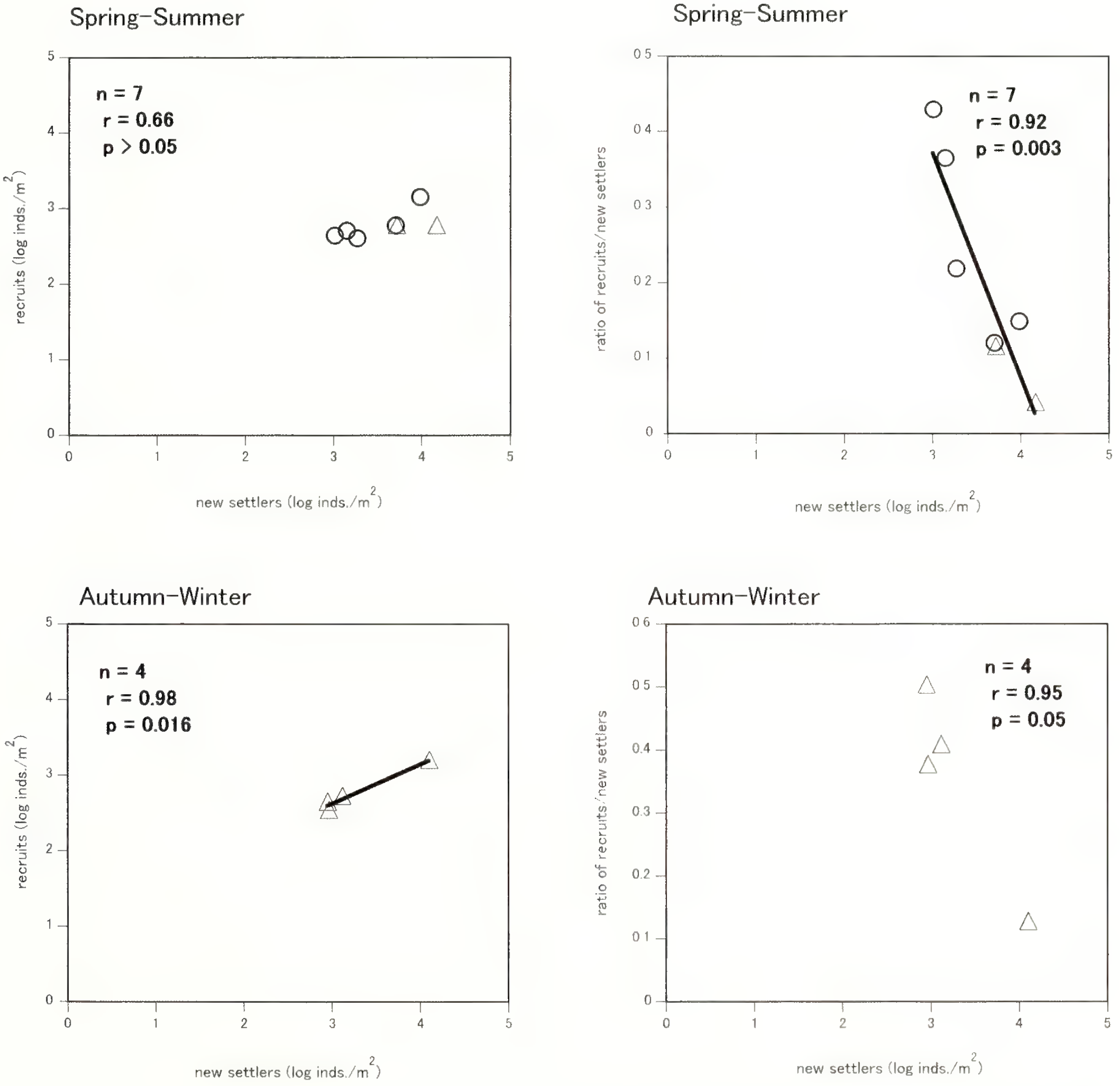

Figure 6. Relationships between densities of new settlers and recruits of *Corbicula japonica* in the Kiso estuaries, central Japan. Upper figures, data for spring-summer cohorts; lower figures, data for autumn-winter cohorts; open circles, data for the Ibi-Nagara Estuary; triangles, data for the Kiso Estuary; n=the number of cohorts.

the Ibi-Nagara Estuary, 5 from the Kiso Estuary), there was a significantly positive correlation between densities of new settlers and recruits in the combined estuaries, but not in each estuary (Fig. 5). There was a significant negative correlation between the density of new settlers and the ratio of their densities (recruits/new settlers) for these estuaries combined and also for each estuary individually (Fig. 5).

The 11 successful cohorts that were divided into two groups, 7 spring-summer cohorts and 4 autumn-winter ones, according to the months with successful recruitment. There was no significant correlation between densities of new settlers and recruits for spring-summer cohorts, whereas there was a significant negative correlation between the density of new settlers and the ratio of their densities (recruits/new settlers) (Fig. 6). The reverse was true for autumn-winter cohorts (Fig. 6): There was a significant positive correlation between densities of new settlers and recruits for autumn-winter cohorts, but there was no significant correlation between the density of new settlers and the ratio of their densities (recruits/new settlers).

Ontogenetic habitat shift of *Corbicula japonica*

Of the cohorts identified in the Ibi-Nagara Estuary, 4 cohorts (i-iv) were successful in reaching shell lengths (12.0 mm) of commercially important individuals (Fig. 3B). Each cohort had a similar spatio-temporal distribution (Fig. 7): new settlers and small individuals were collected mainly in the upper region of the estuary, large and commercially important individuals were found primarily in the central region. Nanbu *et al.* (2005) found an ontogenetic habitat shift during the benthic stages (from new settlers to commercially important individuals) in mixed cohorts of this clam. An ontogenetic habitat shift was also detected within the same cohort, as indicated in Fig. 7. However, this was not true for

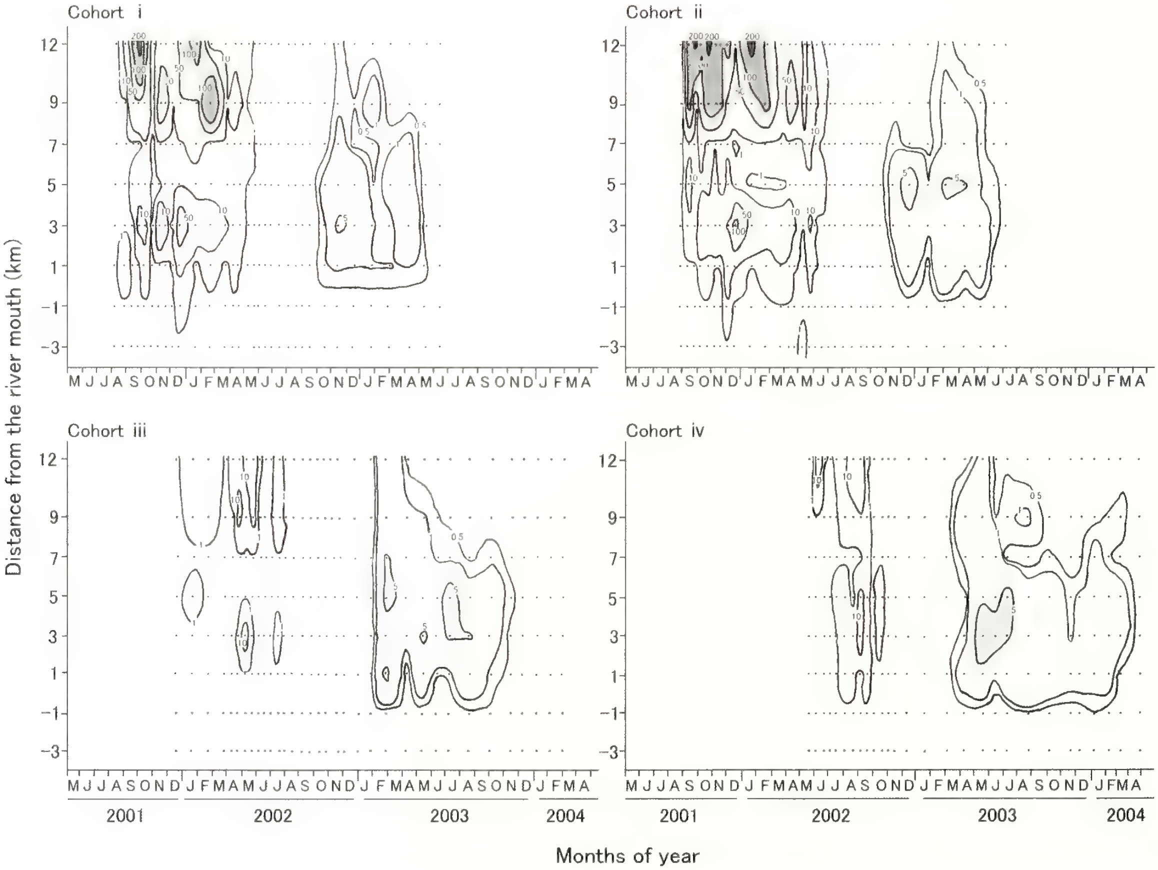

Figure 7. Habitats of different cohorts of *Corbicula japonica* in the Ibi-Nagara Estuary, central Japan. Dots, sampling day/location; solid lines, isopleths of densities of new settlers/small individuals or large/commercial individuals; numerals, density in inds./0.01m^2; gray to black areas, the highest density areas with 50 inds./0.01m^2 or more for new settlers/small individuals and 5 inds./0.01m^2 or more for large individuals. Left and right isopleths in each figure indicate isopleths for new settlers/small individuals and large/commercial individuals, respectively. Open space between isopleths of new settlers/small individuals and large/commercial individuals in each figure is due to the transition between these two groups, as indicated in Figures 3 and 4.

cohorts in the Kiso Estuary. In the Kiso Estuary, 4 cohorts (1-4) were successful in reaching shell lengths of commercially important individuals (Fig. 4B). All cohorts had similar spatio-temporal distributions (Fig. 8): Benthic stages were collected primarily in the upper region of the estuary.

DISCUSSION

As summarized for densities of different life stages of *Corbicula japonica* in Table 1, there was no significant difference in larval densities between the Ibi-Nagara and the Kiso Estuaries through the three-year investigation. This was also true for new settlers (except for 2003) and for large and commercially important individuals (except for 2001). On the other hand, there were significant differences in the density of small individuals between the two estuaries: A higher density was detected in the Ibi-Nagara Estuary than in the Kiso Estuary. Because the local fishermen's union (*e.g.*, Akasuka) gets higher annual catch yields of the clam in the Ibi-Nagara Estuary, putting higher fishing pressure on commercially important individuals in the estuary (Mizuno *et al.* 2005), commercially important individuals may in fact have a much higher density in the Ibi-Nagara Estuary. In each estuary, the density of commercially important individuals was significantly higher in 2002, but there was not a significant difference in the densities of larvae and new settlers between sampling years (Table 1). This suggests that processes affecting benthic stages (new settlers and small individuals), not processes affecting larval settlement and larval supply, may contribute to generating the differences in densities of small individuals between these estuaries. However,

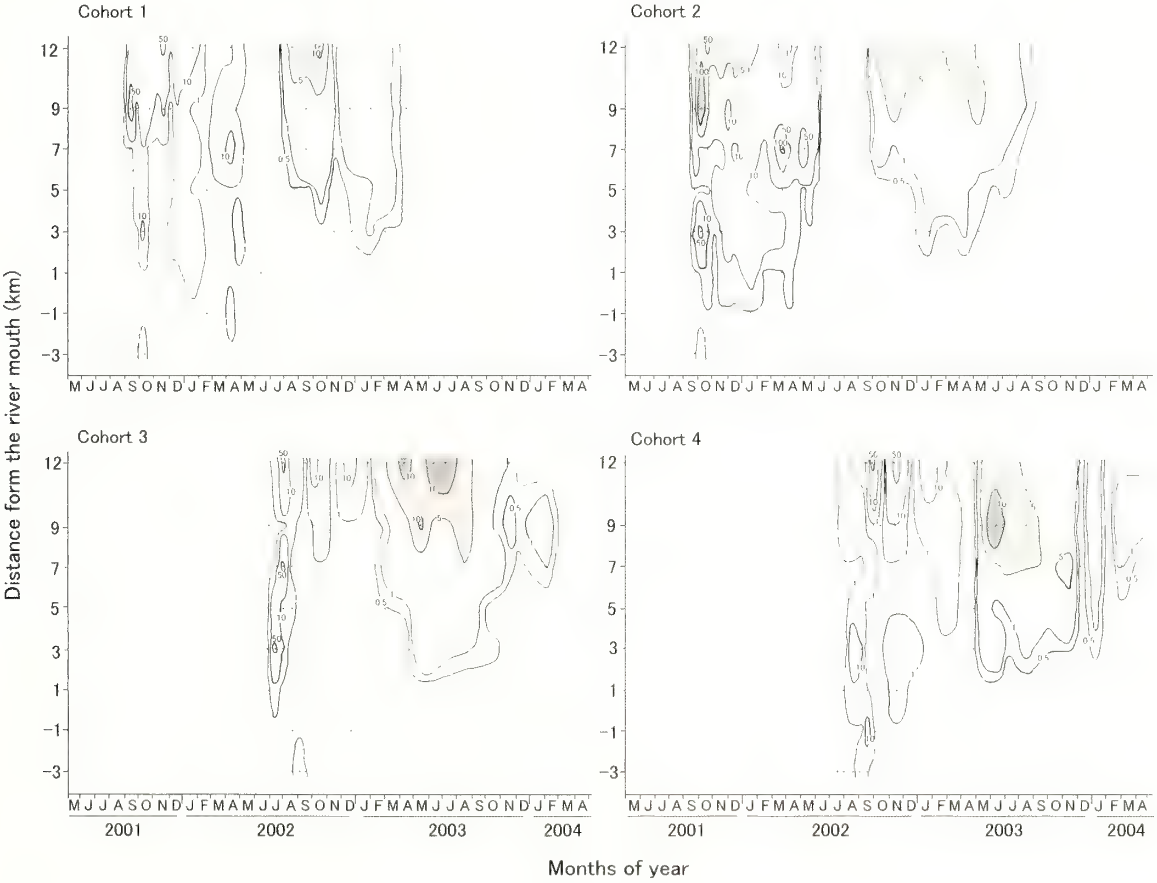

Figure 8. Habitats of different cohorts of *Corbicula japonica* in the Kiso Estuary, central Japan. Dots, sampling day/location; solid lines, isopleths of densities of new settlers/small individuals or large/commercial individuals; numerals, density in inds./0.01m^2; gray to black areas, the highest density areas with 50 inds./0.01m^2 or more for new settlers/small individuals and 5 inds./0.01m^2 or more for large individuals. Left and right isopleths in each figure indicate isopleths for new settlers/small individuals and large/commercial individuals, respectively. Open space between isopleths of new settlers/small individuals and large/commercial individuals in each figure is due to the transition between these two groups, as indicated in Figures 3 and 4.

the difference in densities of small individuals between the estuaries may not contribute to generating the differences in the densities of the successive benthic stages (large and commercially important individuals) between the estuaries.

For populations of *Corbicula japonica* in the Kiso estuaries, there were significant correlations between the density of new settlers and the ratio of their densities (recruits/new settlers) for each estuary and also for the two estuaries combined (Figs. 5-6). The density of new settlers may have a great influence on the density of recruits. This was also true for spring-summer cohorts, but not for autumn-winter cohorts. According to Mizuno *et al.* (2005), annual catch yields of *C. japonica* in the Kiso estuaries are sustained by individuals (new cohorts) reaching commercially viable shell lengths (12.0 mm) of large individuals in spring to summer every year. Densities of these new cohorts drastically decrease in winter due to high mortality caused by fishing pressure, so that density-dependent processes may not operate on autumn-winter cohorts. On the other hand, density-dependent processes may affect spring-summer cohorts because higher densities of new settlers and small individuals were observed in summer to autumn every year. We conclude that densities of large and commercially important individuals were determined by benthic processes, not by larval supply.

It is not immediately apparent why the shift in an ontogenetic habitat of *Corbicula japonica* was detected only in the Ibi-Nagara Estuary. Nanbu *et al.* (2005) also reported the occurrence of a similar ontogenetic habitat shift for mixed cohorts in the Ibi-Nagara Estuary. They proposed alternative scenarios to explain this shift: (1) The shift may be generated by tidal/diurnal/seasonal/ontogenetic migration using the byssus or other means, as observed in many common bivalves (Hamada and Ino 1954, Sigurdsson *et al.* 1976, Prezant and Chalermwat 1984, Lane *et al.* 1985), particularly in light of the salinity sensitivity of *Corbicula japonica* during ontogeny (Saito *et al.* 2002, Kuwabara and Saito 2003), (2) The shift does not occur within the same cohort; habitats may differ depending on cohort (*i.e.*, the site-specific mortality may differ depending on benthic stage), so that the shift only appears to occur within the same cohort; and (3) The shift does not occur within the same cohort, and the site-specific mortality may differ depending on benthic stage, so that the shift appears to occur within the same cohort. Because of the cohort separation observed in the present study, indicating the occurrence of an ontogenetic habitat shift within the same cohort and because all benthic cohorts had a similar distribution pattern for each estuary, scenario 2 may be rejected. However, we cannot evaluate scenarios 1 or 3 unless we measure the site-specific mortality in the Ibi-Nagara Estuary.

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Investigation in the laboratory of mucous trail detection in the terrestrial pulmonate snail *Mesodon thyroidus* (Say, 1817) (Mollusca: Gastropoda: Polygyridae)*

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Abstract: Many gastropods, including limpets, periwinkles, and mud snails, detect and follow mucous trails. The stylommatophoran pulmonate snail *Mesodon thyroidus* follow conspecific trails in the field, potentially following in the direction they were laid, as has been demonstrated for other pulmonates. This study investigated whether individuals of *M. thyroidus* directionally follows conspecific trails, and whether substrate type or incline influences trail following. Trail following was quantified on plexiglas and glass surfaces at horizontal, vertical, and 45° inclines. On horizontal plexiglas surfaces, 36% of *M. thyroidus* followed a marker trail made by a conspecific (n = 11). On horizontal glass surfaces, 45% of the snails followed a marker trail (n = 20). On glass (all inclines combined) 75% of snails that followed a conspecific trail followed it in the same direction it was laid (n = 60). On plexiglas (all inclines combined) 86% of trail-following proceeded in the direction the trail was laid (n = 33). The difference in the results across the two substrates could indicate a behavioral reaction to the chemical difference of the substrates. Preliminary observations of tentacle movements and of the mucous trails indicate that previously laid trails can be detected before the foot of the following snail contacts the marker trail.

Key words: trail following, mucus, chemoreception, behavior

Moving snails leave mucous trails that can be detected by other organisms, including other snails. Many snails can detect or follow mucous trails of conspecifics and non-conspecifics (Cook 2001). Mucous trail following is used in homing, finding food sources and mates, and forming aggregations (Chase 1986, Tankersley 1989, Cook 2001). Gastropods often move faster on previously-laid mucous trails than on bare substrate (Wareing 1986, Erlandsson and Kostylev 1995) and can detect and respond to the trail's age as well as the physiological state of the individual that left it, avoiding trails left by stressed individuals (Edwards and Davies 2002). Understanding this behavior in gastropods could assist with conservation of endangered species and control of invasive species.

Most pulmonate gastropods have two pairs of tentacles that are used in chemoreception and to follow mucous trails (Chase 1986, Lemaire and Chase 1998). Both the oral (anterior) and optic (posterior) tentacles may be used when following mucous trails, and to detect odors associated with the trail (Chase 1986, Stirling and Hamilton 1986). Chase and Croll (1981) found that the giant African land snail *Achatina fulica* Bowdich, 1822 primarily uses its oral tentacles for following substrate-bound mucus, while the optic tentacles are used for tracking airborne odors. While tracking airborne odors, snails have been observed to hold their optic tentacles at a characteristic angle, around 90° in the horizontal plane with respect to each other (Lemaire and Chase 1998, Davis 2004), which may allow the snail to compare information from its right side to its left side. This tentacle position may also facilitate trail-following. Trails contain information that can be detected by chemosensory and mechanosensory receptors (Denny 1989). Trail-following may be a primary mechanism to find mates, given that most terrestrial pulmonates cannot self-fertilize despite being hermaphroditic (Stanisic 1998).

Mesodon thyroidus (Say, 1817) is a species of terrestrial snail native to the eastern United States (Burch 1962, Hubricht 1985) and is common in Lawrence, Kansas, U.S.A. (Pilsbry 1940, Leonard 1959). It eats plants and fungus (Burch 1962) and, in Kansas, is often found in large groups (> 100 individuals in 1 m^2). Pearce (1990) showed that individuals of *M. thyroidus* follow conspecifics by marking the paths of snails in the field (using the "spool and line" technique), but did not examine mucous trails or the role of trail-following.

To follow up on Pearce's (1990) study I asked how often individuals of *Mesodon thyroidus* follow conspecific trails and if they can follow in the direction that the trail was laid. I quantified trail-following on two different substrates (plexiglas and glass) at three different inclines (horizontal, vertical, and 45°). Snails encounter many inclines in their natural environment, and I expected that substrate incline would not influence trail-following. However, snails often crawl in straight lines up vertical surfaces, which could change the tortuosity (or curviness) of the trail by incline. I also explored the effects of trail remnants on trail following because plexiglas and glass plates retain mucus differentially after cleaning. The goals of this study were to determine: (1) how often the polygyrid snails of *Mesodon thyroidus* follow mucous trails made by conspecifics, (2) if the substrate incline (horizontal, 45°, and vertical) affects trail following, and (3) the effects of trail remnants on trail following.

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METHODS

Approximately 100 specimens of *Mesodon thyroidus* collected from a compost pile in Lawrence, Kansas, U.S.A., were brought into the laboratory. Sexually mature snails (n = 26), determined by the presence of a lip on the aperture, were kept for at least 7 days in individual boxes with damp paper towels (for moisture), and a container of moist peat moss at least 2 cm deep to provide a substrate for egg-laying. Snails were kept at room temperature (20°C) and in natural light near windows in the laboratory, and were fed carrots or lettuce on alternate days. All snails used in this experiment can be found at the University of Kansas Natural History Museum, catalog numbers 002437-002462.

To test whether a snail could detect a conspecific mucous trail, the first snail—designated the "marker" snail—was allowed to crawl on a 20 cm × 20 cm pane of picture glass. In each trial a marker snail was centered at an edge of the pane of glass facing the center and allowed to crawl until it reached an edge. Trials were stopped if a snail did not move for more than 5 min or if the mucous trail was not straight for at least one body length. After the snail reached the edge of the glass it was removed. The glass was then rotated 90° (randomized between clockwise and counterclockwise) and a second (experimental) snail was placed at least one body length from the trail at approximately 90° to the marker trail. The experimental snail was allowed to crawl until it reached the edge of the glass or was removed due to lack of movement; the trial was discarded if the snail did not move for at least 5 min. Trials were conducted on horizontal, sloped (45° from the horizontal), and vertical panes to test if the incline of the substrate affected trail following (both marker and experimental snails crawled on panes at the same incline). All trials were videotaped to facilitate observation of tentacle movements, their angle, and to confirm the paths of the snails. After the experimental snail was removed, the mucus was allowed to dry on the glass before being stained (see below). To ensure independent trials, each pair of marker and experimental snails was used only once. Individual shells were numbered with a paint pen.

The trails were stained by soaking the glass panes for 1-5 min in a suspension of carbon particles (laser printer toner) in distilled water (Karowe *et al.* 1993). These stained trails were photocopied for record keeping. Afterward, the glass plates were soaked for 5 min in 5% acetic acid, washed with soap and distilled water, rinsed with distilled water, soaked for 20 min in 3% sodium hypochlorite, and rinsed six times with distilled water. This cleaning process removed all traces of the mucus from the glass, as confirmed by exposure to carbon particles.

To test for the effects of trail remnants on trail following, plexiglas substrates were used. For plexiglas substrates (20 cm × 20 cm), the procedure was similar to that used with glass, with two exceptions. Snails were kept in groups in containers rather than individually, and each group of snails was tested against another group. Second, the plexiglas was washed with soap and distilled water, rinsed with distilled water, and then rinsed with 95% ethanol. The porous plexi-

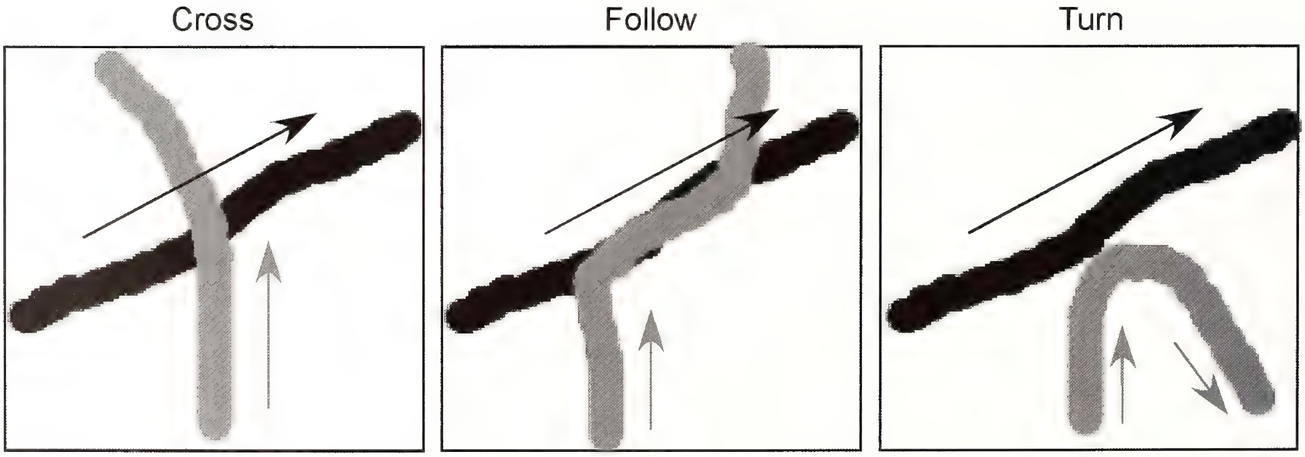

Figure 1. Categories used to score snail behavior; marker (first) trail is black, experimental (second) trail is gray.

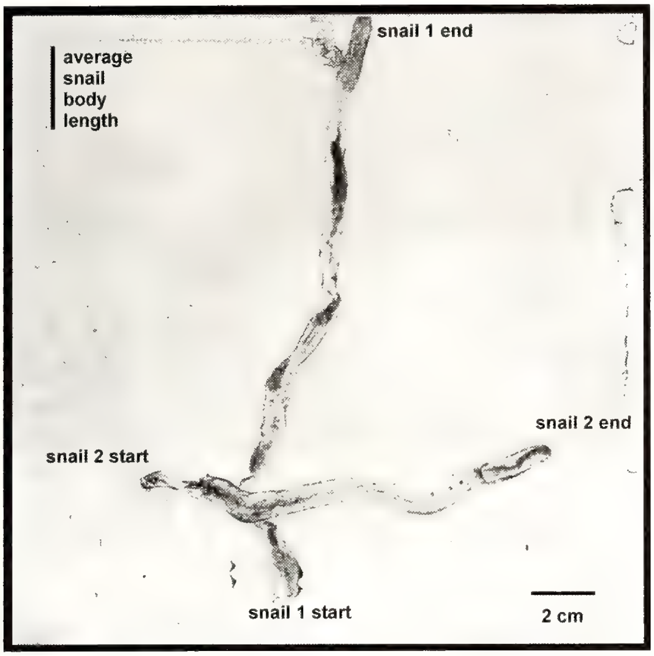

Figure 2. Example of stained trails showing a cross response.

glas substrate retained portions of previous trails. Thus, experimental snails on plexiglas were tested in the presence of remnant trails as well as a marker trail. The presence of remnant trails was confirmed by staining with carbon particles after these trials were conducted. Some of these trials were traced onto acetate sheets after being stained with colored chalk before the carbon particle method was perfected. All other procedures were the same.

For glass and plexiglas substrates, the behavior of each experimental snail was analyzed by examining its mucous trail. I characterized each trial as belonging in one of three categories: cross, follow, and turn (Fig. 1). A cross was defined as any overlap by an experimental trail of less than one body length of a marker snail trail (Fig. 2). A follow was defined as an overlap of at least one body length of marker and experimental trails (Fig. 3). A turn was defined as a complete turn (180° ± 15°) of an experimental trail occurring just before or adjacent to a marker trail (Fig. 4). Both turning and following were considered to be responses because the snail appeared to have an obvious behavioral response to a marker snail's trail. Although crossing a trail was considered a non-response behavior, it does not imply that the snail did not detect the trail.

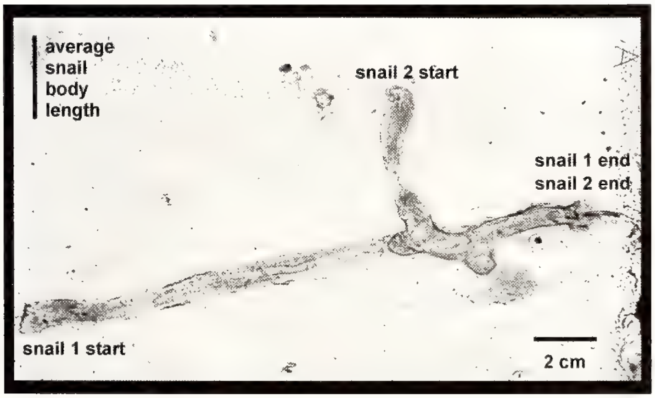

Figure 3. Example of stained trails showing a follow response.

To quantify how often individuals of *Mesodon thyroidus* follow mucous trails, the counts of the behavioral results of trail encounters were compared by category to two null models. These results were also used to test for a difference by substrate incline. Fisher's exact test (Sokal and Rohlf 1995) was used to test the grouped results of response (turn/follow) and non-response (cross) categories against the null models. Because of low counts the results were grouped as response (turn/follow) and non-response (cross) rather than as the three scored categories. The first null model, which was used on both plexiglas and glass trials, was generated by scoring trails against randomly drawn straight lines rather than against the marker trails. These lines were drawn between two randomly chosen points along the edges of a grid that was size-matched to the substrates. The lines were then scored against an experimental snail's path to generate expected responses for a "null" trail. I used these scores as the

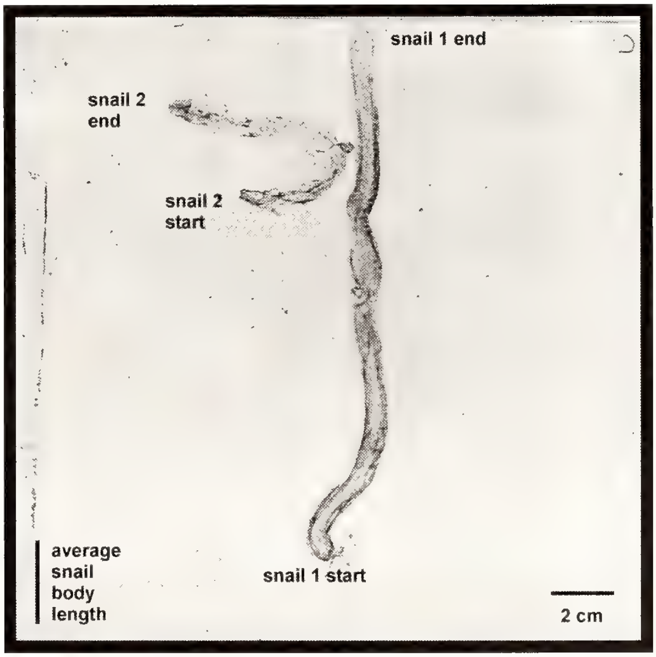

Figure 4. Example of stained trails showing a turn response.

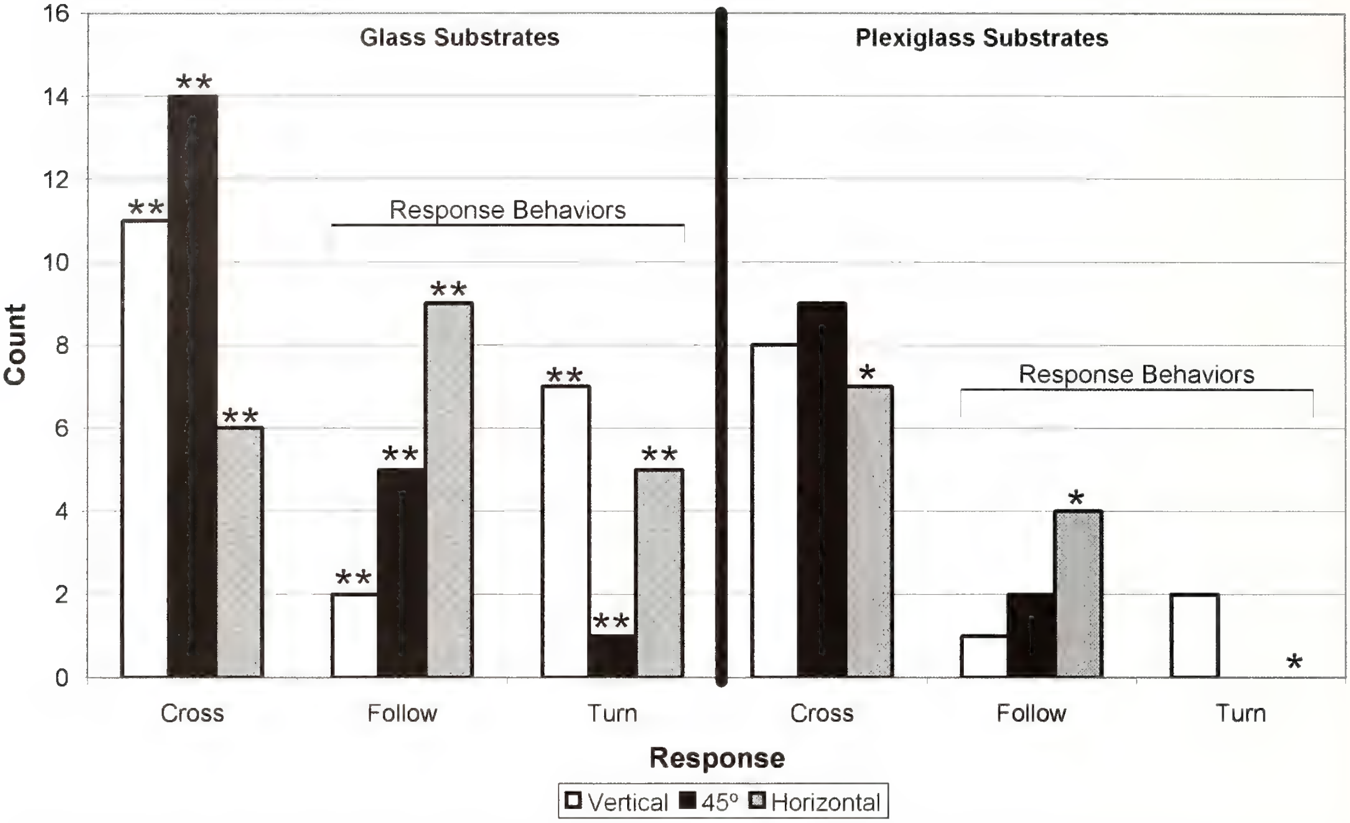

Figure 5. Response of experimental snail to marker trail on glass and plexiglas substrates. On both substrates, snails were able to detect trails at all substrate inclines and followed most often on horizontal surfaces. * = Results by incline are significantly different than the straight line null ($\alpha = 0.05$) with straight line nulls. ** = Results by incline are significantly different than the straight line null ($\alpha = 0.05$) with both "marker" trail and straight line nulls.

expected values in Fisher's exact test. The second null model used on both plexiglas and glass trials quantified trail crossing, following, and turning for two overlaid marker trails, selected randomly. These trails were overlapped by randomly orienting the "null" marker substrate (0°, 90°, 180°, and 270° from its original orientation) and then lining up the corners of the substrates between the two trials. The two marker trails were then scored. The results from the second null model generated an additional set of expected values. These expected results were tested using the same statistics as the "null lines." The second null model did not work as well for the plexiglas substrate because many trials were recorded on acetate sheets that did not include information on snail orientation or trail location on the substrate. This meant that not all plexiglas trials could be tested the same way. These problems make the second null model much less reliable for the plexiglas substrate than the straight line null model. However, both models show the same trend with the results.

To analyze the path of the snail trails, I wrote a program in Visual Basic for Applications (VBA—Microsoft) in Excel (Microsoft) to calculate the length, tortuosity, and angle of approach of the tracker snail to the marker path (Davis 2005). Paths were digitized using Didger (v. 2, Golden Software, Inc.) and uploaded into the VBA program as two-dimensional points. The total length of the path was calculated by adding successive line segments. Tortuosity, a measure of the curviness of the trail, was calculated by taking the ratio of the total length of the path of the snail to the straight line distance between the first and last points (start and stop points of the trail). High tortuosity in the marker trail could hamper the experimental snail's trail-following ability. A general linear model (GLM) was used to test the tortuosity ratio (beginning-to-end distance/total distance) against both incline of substrate (vertical, horizontal, 45°) and behavioral response (cross, follow, turn). GLM was also used to test behavioral response of the snail against tortuosity (Sokal and Rohlf 1995). The angle between paths was determined by calculating the angle of approach of the experimental snail in relation to the marker snail. These angles were divided into two groups—those that were within 45° of

Table 1. Expected values for Fisher's exact tests generated from the two different null models.

Trials on glass (single trail)

Straight "Null" Lines	Cross	Follow	Turn	"Marker" trail as null	Cross	Follow	Turn
Incline				Incline			
Vertical	43	6	0	Vertical	56	2	0
Horizontal	41	5	2	Horizontal	57	3	1
45°	47	2	0	45°	63	4	3

Trials on plexiglas (most recent trail)

Straight "Null" Lines	Cross	Follow	Turn	"Marker" trail as null	Cross	Follow	Turn
Incline				Incline			
Vertical	39	2	0	Vertical	34	5	1
Horizontal	31	1	1	Horizontal	33	4	1
45°	48	2	0	45°	27	4	1

perpendicular to the marker trail and those that were within 45° of parallel to the marker trail. A G-test was used to determine if the angle of approach of the experimental trail was independent of the behavioral response of the experimental snail (Sokal and Rohlf 1995). In addition, I tested if the angle of approach between trails affected the directionality of following by using a Chi-squared test (a G-test could not be used because of counts of zero).

RESULTS

Individuals of *Mesodon thyroidus* were able to detect and follow trails on both substrates and at all inclines, but trail-following diminished as the inclination approached vertical (Fig. 5). At each inclination, snails followed more trails on glass than on plexiglas. On glass surfaces, snails responded to conspecific trails significantly more often than was predicted by either null model at all inclinations (Fisher's Exact Test, $\alpha = 0.05$, Tables 1 and 2), but differences between inclinations were significant (Fig. 5). An individual snail did not necessarily show the same response to every trail encountered. Of the snails that followed on glass surfaces, 75% of them followed in the direction in which the marker trail had been laid. On plexiglas substrates, the behavioral responses indicate that snails detected trails at all inclinations, even in the presence of remnant trails. However, responses to marker trails were statistically significant ($\alpha = 0.05$) for horizontal surfaces only (Table 2). Eighty-six percent of snails that followed a conspecific trail did so in the same direction in which the trail was laid. The plexiglas null model using superimposed marker trails was problematic because some of these trials were conducted before the carbon particle method was developed and the trails were traced without recording their orientation on the plexiglas.

Observations of optic tentacles showed that optic tentacles were often held parallel to the substrate and oral tentacles alternately touched the substrate while the snail was at rest and when it was moving. A snail was often seen lifting its head from the substrate and moving its head from side to side while its tentacles remained stationary with respect to the head.

On glass substrates, the results of the trail analysis (using the VBA program) indicated that there was not a significant difference between the tortuosity of the trail and the behavioral response (from GLM of tortuosity by behavioral response and snail order: Response [Cross, Follow, Turn]:

Table 2. Results of Fisher's exact test. * = results that are significantly different than the null ($\alpha = 0.05$), indicating that snails are responding to trails.

With straight line "trails" as null	Incline		
Probability	Vertical	45°	Horizontal
2-tailed, single trail (glass)	0.0076*	0.0059*	0.0002*
2-tailed, most recent trail (plexiglas)	0.0574	0.1455	0.0269*
With "marker" trail as null	Incline		
Probability	Vertical	45°	Horizontal
2-tailed, single trail (glass)	0.0004*	0.0355*	4.553×10^{-8}*
2-tailed, most recent trail (plexiglas)	0.3848	1.0	0.1785

F = 0.30, df = 2 $p = 0.744$, Snail Order: F = 0.73, df = 1 $p = 0.395$, Interaction [Snail Order*Response]: F=0.41, df = 2 $p = 0.662$). On plexiglas, there was a significant difference between the tortuosity of the trail and the behavioral response (from GLM of tortuosity by behavioral response and snail order: Response [Cross, Follow, Turn]: F = 11.26, df = 2 $p = 0.0$, Snail Order: F = 2.03, df = 1 $p = 0.159$, Interaction [Snail Order*Response]: F=3.66, df = 2 $p = 0.032$). A graphical representation of the tortuosity data from glass can be seen in Fig. 6. One trial (45° glass, cross), however, could not be digitized from the carbon visualization and so could not be included in the trail analysis using the VBA program. Similarly, on glass substrates, there was no significant correlation of angle difference (between marker and experimental snail) and behavioral response (cross, response) (G = 0.86, $p = 0.35$, df = 1) for the angle between the two trails. However, on plexiglas substrates there was a significant correlation of angle difference and behavioral response (G = 13.5, $p < 0.005$, df = 1). All but one of the follow responses on plexiglas occurred with an angle that was within 45° of parallel to the trail. With the subset of snails that followed on both substrates, there was no significant difference between the angle difference (between marker and experimental snail) and directionality of the follow response (right way, wrong way) (glass $\chi^2 = 0.042$, $p = 0.838$, df = 1; plexiglas $\chi^2 = 0.194$, $p = 0.659$, df = 1). Table 3 summarizes the results of the trail analysis.

DISCUSSION

Individuals of *Mesodon thyroidus* were able to detect conspecific mucous trails at all three substrate inclines tested in this study (horizontal, 45°, and vertical). The substrate type and incline had the greatest effects on the behavioral responses of the snails. The effect of incline is interesting given that snails encounter all inclines of substrate in their environment. Individuals of *M. thyroidus* did not respond to

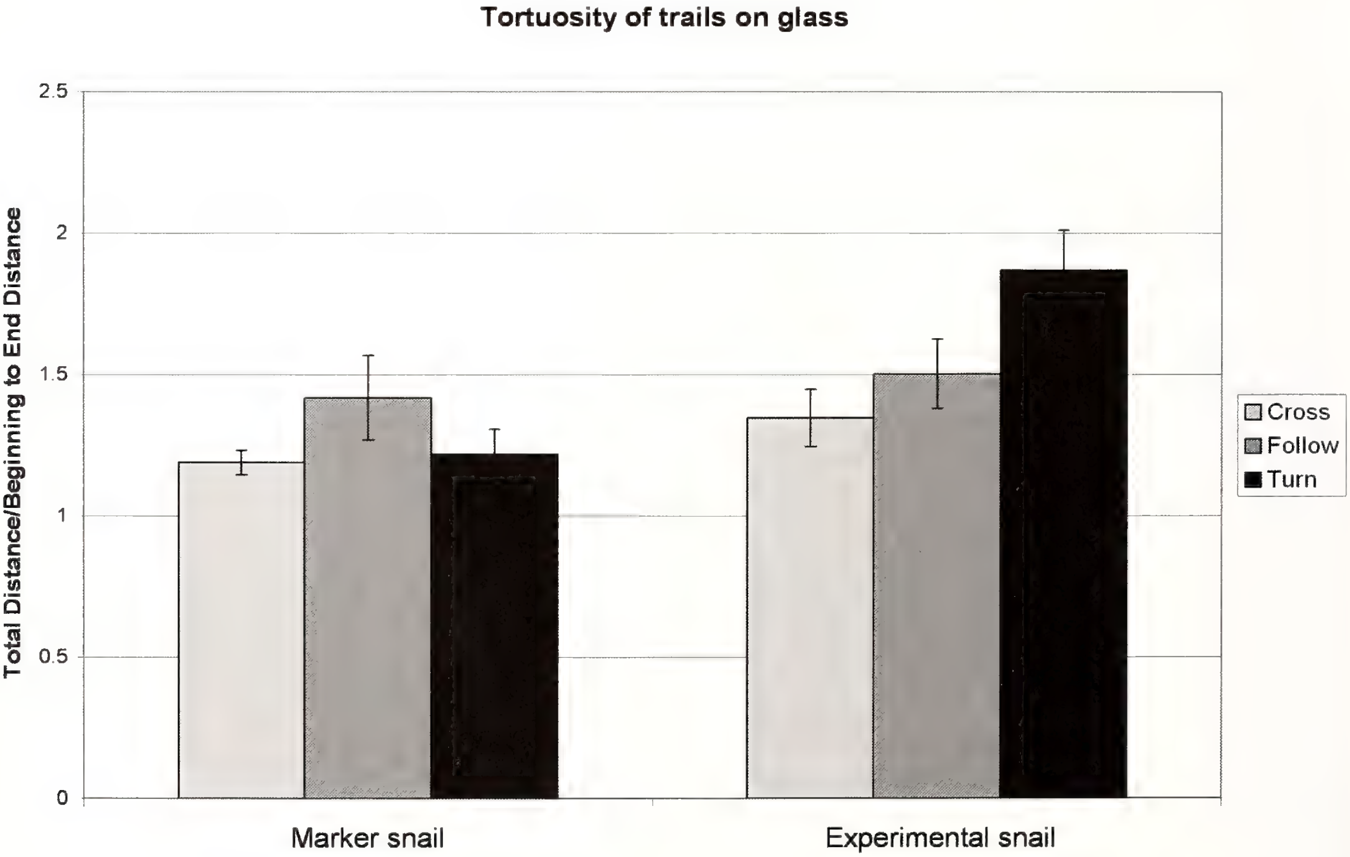

Figure 6. Results from VBA analysis of snail paths on glass substrates. One outlier data point (experimental cross) was excluded because the trail returned to the same place it started, causing the ratio of total distance/beginning to end distance to be very large. Error bars indicate plus/minus one standard error.

Table 3. Statistics on the results of quantitative analysis of trails using the VBA program. *, results that are significantly different than the null ($\alpha = 0.05$)

Statistical Test	Substrate	Results						
General Linear Model (GLM) of tortuosity of trail by behavioral response and snail order	Glass	Source	DF	Seq SS	Adj SS	Adj MS	F	P
		Response	2	22.61	22.61	11.30	0.30	0.744
		Snail	1	55.27	27.79	27.79	0.73	0.395
		Response*Snail	2	31.48	31.48	15.74	0.41	0.662
		Error	112	4262.97	4262.97	38.06		
		Total	117	4372.32				
	Plexiglas	Source	DF	Seq SS	Adj SS	Adj MS	F	P
		Response	2	34.682	34.682	17.341	11.26	0.000*
		Snail	1	0.217	3.134	3.134	2.03	0.159
		Response*Snail	2	11.276	11.276	5.638	3.66	0.032*
		Error	60	92.414	92.414	1.540		
		Total	65	138.588				
G-test of the angle difference by behavioral response (cross/follow)	Glass	$G = 0.86$, $p = 0.35$, df =1						
	Plexiglas	$G = 13.5$, $p < 0.005$*, df =1						
Chi-squared test of the angle difference by following direction	Glass	$\chi^2 = 0.042$, $p = 0.838$, df = 1						
	Plexiglas	$\chi^2 = 0.194$, $p = 0.659$, df = 1						

every trail encountered in this experiment, as indicated by the cross responses. On glass substrates (single mucous trail) no significant effect of inclination of substrate was seen on behavioral response. On plexiglas substrates (most recent mucous trail) only the horizontal incline showed statistically significant response behavior compared to the straight null lines (which were a better null for these data). Cain and Cowie (1978) found that snails with flatter-spired shells were more likely to be active on horizontal surfaces, which could explain why the horizontal incline showed statistically significant response behavior in both experiments. However, these snails are often found climbing trees in the southern part of their range (personal observations, Davis *et al.* 2004). The non-significance of the results on plexiglas could be due to the presence of remnant trails. But it could also be an artifact of the small counts due to sample size ($n = 11$ for each incline) or a difference in chemical composition of the substrate. I did not observe that snails had any potential difficulties in climbing on plexiglas or any other behavioral reaction to indicate a difference on plexiglas versus glass. The results on plexiglas were important in demonstrating that *M. thyroidus* can detect the most recent mucous trail when remnant trails exist in the environment. Staining of plexiglas showed physical evidence of remnant trails, which may or may not have been detected. Unfortunately, the presence of remnant trails on what was believed to be "clean" plexiglas was only confirmed by staining with carbon particles after this experiment was conducted. However, these results can be used as preliminary data on the effect of trail remnants on trail following. As expected, this experiment verified the field experiments of Pearce (1990), in which many mucous trails were present in the environment and conspecific following was observed.

The mechanisms used by snails to detect trails are not well understood (Stirling and Hamilton 1986, Denny 1989, Erlandsson and Kostylev 1995) but the turn response I observed indicates that trails can be detected before the foot of the following snail contacts the marker snail's trail. The tentacles of snails can be used to track odors by both tropotaxis and anemotaxis (Chase and Croll 1981, Lemaire and Chase 1998). In the terrestrial pulmonate *Achatina fulica*, Chase and Croll (1981) observed that both pairs of tentacles are used to orient to concentration gradients and to mucous trails. I was able to confirm Chase and Croll's (1981) observation that both pairs of tentacles were moved and seemed to be used when following trails. It is possible that each snail could detect every trail it encountered in the experiment but responded only to some of them, which is why I observed many more cross responses than follow or turn responses.

In this study, there were clear differences between the behavioral results obtained across the two tested substrates. All of the snails tested against the glass substrate were individually housed. However, the snails tested on plexiglas were kept in group containers, and it is possible that recent mating of the marker snail could be assessed through the mucous trail and effected the response behavior of the experimental snail. Feeding time was consistent across all snails. Other studies with non-pulmonate snails have shown that the physiological state of the individual, such as stress due to starvation, can be assessed (Edwards and Davies 2002) by a following snail. I do not think that food-stress was a factor in my results.

If we understand the mechanisms that are used to detect and follow trails in pulmonate snails then it is possible that we can use this knowledge to aid in conservation. For example, the carnivorous pulmonate snail *Euglandina rosea* (Férussac, 1821) uses mucous trails to find its prey (Cook 1985, Davis 2005) and has been implicated in the decline and extinction of many native snails on the islands of Hawaii, Tahiti, and Moorea among others (Cowie and Robinson 2003). Understanding the mechanisms of trail detection could be used to create false trails leading to traps, controlling the pest species, if we can assume that those mucous trails are followed in the direction that they were laid.

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RESEARCH NOTE

Confirmed absence of a relict population of *Gonidea angulata* (Lea, 1838) (Mollusca: Bivalvia: Unionidae) in Colorado

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Abstract: The diversity of freshwater mussels in Colorado is low compared to other regions of the U.S.A., with only three extant species (down from seven a century ago). The western ridged mussel (*Gonidea angulata*) occurs in Pacific Coast drainages from British Columbia to California and eastward to Idaho and Nevada. It has been reported from Colorado based on a single museum specimen from Clear Lake, representing a significant range expansion for this species. During extensive recent surveys, I was unable to pinpoint this locality and regarded it as questionable. Examination of the specimen and locality data indicated this specimen was collected from Clear Lake, Lake County, California.

Key words: freshwater mussels, Unionidae, Colorado, distribution, range

Studies of freshwater mussels in the Rocky Mountain region are rare compared to other regions of North America. Historical surveys were conducted by Cockerell (1889, 1927), Ellis (1916), Ellis and Keim (1918), and Henderson (1907a, 1907b, 1912, 1924). More recent surveys include Brandauer and Wu (1978), Herrmann and Fajt (1985), and Wu (1989).

Gonidea angulata (Lea, 1838) is a freshwater mussel (family Unionidae) belonging to a monotypic genus confined to Pacific drainages of northwestern North America (Graf 2002). Its historical range extended from southern British Columbia to southern California and eastward to Idaho and Nevada with extant populations in southwest Washington, northwest Oregon, continuously from southwest Oregon south to southern California, as well as interior Washington and Oregon, southern Idaho, and northern Nevada (Ingram 1948, Taylor 1981, COSEWIC 2003, NatureServe 2004).

I published a distributional guide to the few remaining freshwater mussels in Colorado (Cordeiro 1999) as well as some short notations on distribution of freshwater bivalves in the state (Cordeiro 1998, Cordeiro and MacWilliams 1999). Distributional data included records from museum collections, published and unpublished literature, and field surveys. Prior surveys revealed six species in the state: *Anodontoides ferussacianus* (Lea, 1834), *Lampsilis siliquoidea* (Barnes, 1823), *Lampsilis teres* (Rafinesque, 1820), *Pyganodon grandis* (Say, 1829), *Strophitus undulatus* (Say, 1817), and *Uniomerus tetralasmus* (Say, 1831). A seventh species, *Lampsilis ventricosa* (Barnes, 1823) was cited by Henderson (1907a) for Lodgepole Creek in the northwest corner of the state but this species has been synonymized under both *Lampsilis ovata* (Say, 1817) and *Lampsilis cardium* Rafinesque, 1820. Presently, only *A. ferussacianus*, *P. grandis*, and *U. tetralasmus* are extant in Colorado (Cordeiro 1999). Additionally, I cited an unconfirmed record of *Gonidea angulata* (Lea, 1838), based on a single specimen in the Florida Museum of Natural History (FLMNH 65292) collected from "Clear Lake, Colorado." I was unable to survey Clear Lake due to time, distance, and some confusion over its exact location. There are three different Clear Lakes in Colorado: in Delta and Gunnison Counties (Colorado River Basin), as well as in San Juan County (San Juan River Basin). None are even remotely close to any current or historical occurrences of freshwater mussels in Colorado nor are they within any Pacific drainages where *G. angulata* is typically found. Surveys in western Colorado for freshwater molluscs (including mussels) in 2003 (Sovell and Guralnick 2004) and 2004 (J. Sovell, pers. comm.) have failed to find this or any other species of freshwater mussel.

Other recent surveys have detected *Gonidea angulata* in the Humboldt River drainage (Lahonta Basin) in northern Nevada (Hovingh 2004). Smaller individuals found downstream in Carlin (Hovingh 2004) indicate this population may be increasing and may have been overlooked in previous surveys as this area historically contained only *Anodonta californiensis* Lea, 1852, in 1912 and 1939 (Walker 1916, Jones 1940). Despite early reports by Henderson (1924, 1929, 1936) for Utah and Montana, more recent surveys in these states have failed to find any individuals of *G. angulata*

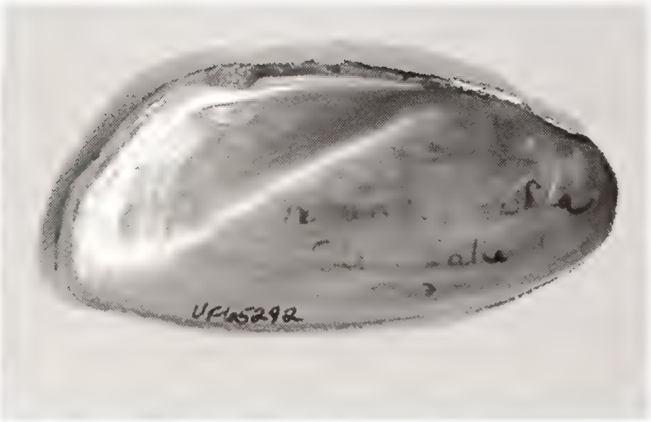

Figure 1. Florida Museum of Natural History specimen lot FLMNH 65292 of *Gonidea angulata* (shell length approximately 70 mm). Photo by John Slapcinscky, FLMNH.

(Chamberlin and Jones 1929, Jones 1940, Oliver and Bosworth 1999, Gangloff and Gustafson 2000, Lippincott and Davis 2000).

Clear Lake, occupying several towns in Lake County, California, is the state's second largest freshwater lake and is likely the proper locality for the FLMNH specimen lot of *Gonidea angulata*. The presence of *G. angulata* in Clear Lake is documented by Taylor (1981: 143) and by museum specimens from the Florida Museum of Natural History (FLMNH 4234) and United States National Museum (USNM 26094). Examination of FLMNH 65292 (Fig. 1) revealed writing on the interior left valve, "*N. angulata* Clear Lake Cal", with the "a" not quite making a complete circle and having a very short tail. The specimen was collected by C. Mohr, who deposited other specimens in the Florida Museum of Natural History from California (Monterey, Purissima, San Diego, San Francisco, and Tomales Bay) but not from Colorado (J. Slapcinsky, pers. comm.). This confirms the locality as Clear Lake, California, and not Clear Lake, Colorado.

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BOOK REVIEW

The Caribbean Land Snail Family Annulariidae: A revision of the higher taxa and a catalog of the species by G. T. Watters (2006). Backhuys Publishers, Leiden, The Netherlands. vii + 557 + 9 + 4 pp. With 9 black-white-figures and 57 maps. ISBN: 90-5782-155-9.

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Although the Annulariidae immediately attract the attention of every naturalist visiting the Caribbean region by their beauty and amazing diversity, the tremendous number of taxa - Watters accepts half of the about 1,400 described names as valid species or subspecies - and the difficult access to reliable information prevent the enthusiast from entering deeper into the subject. It would certainly be too high an expectation to find all these problems answered in this new book, but Watters' bulky 577-page hardcover contribution presents the most comprehensive compilation on the Annulariidae to date, including all traceable taxa from subspecies to family level. It intends " . . . to bring all available information on the family together, to provide an overview of the group including their morphology, zoogeography, evolution, and systematics" (p. 1). The aim is certainly met with regard to the annotated taxonomic list, which comprises the lion's share of the book with about 540 pages. On the other hand, the claim – if carefully read – also makes clear what might not be expected and consequently will not be found: substantial new research results on the topics mentioned. So, except for the historical and nomenclatural section (6 pages), the remaining 13 general pages are not ambitious and give the impression that the book results from diligent library and museum collection work, but lacks the inspiration of fieldwork. Who else could overlook to tell about the exceptional "walking" of Annulariidae in a general account and only mention it by chance in a discussion of phylogenetic relationships? The very little but precious information cited on anatomy remains similarly isolated when, in another context, the author seriously discusses the published speculation ("deserves further consideration") that decollation might provide a breathing device at the very top of the shell by a more porous closure (Rees 1964) which, concluding from general anatomy, would require that the digestive gland or parts of the reproductive system spontaneously take up a function as respiratory epithelium!

Apart from some weaknesses in the section of general information, the strength and value of Watters' contribution consists in the immense bibliographic work, the hunt for type material in museum collections and accompanying historical information, and the clarification of entangled, often-nightmarish nomenclatural problems.

The species account (with 434 pages about 75% of the book) includes data on the original reference; the type locality and known range, the depository of type material, if located; the current systematic assignment; and widely accepted synonyms. Herein it stays in the correctly given limits of a pure catalog, which is appreciated as the most realistic way to approach a review at the family level, added by the "extra" of etymological information for the reader interested in history of science. The listing of species by country under each genus is a most helpful addition for students of specific geographic areas.

Unfortunately, and this being inexcusable for author and publisher, the alphabetical arrangements of genera and species fail to compensate for the lack of an index to the thousands of names included in the text, rendering all synonyms, subgenera, and subspecies not searchable. The "Outline of higher taxa" provides only limited help at the supraspecific level.

The lack of figures is most unfortunate. Especially in times of digital photography, it is astonishing that not a single (!) member of the Annulariidae is figured on these 577 pages. Only the character that is least necessary to figure is illustrated, with images of 9 opercula hidden at the end of the book instead of accompanying the respective text, while characters that are difficult to describe – such as hidden breathing devices of astonishing shapes and details of radular teeth – remain to the imagination of the reader. At the very least, illustrations of the type species or typical representatives of the 56 genera (and perhaps 31 subgenera) would have greatly improved the contribution, especially because almost all descriptions and delineations of the supraspecific taxa refer to conchological characters.

The "revision" as announced in the misleading title disappoints in the sense of a new scientific analysis. Without intention to judge the currently proposed classification of the Annulariidae and despite thorough reading I was unable to find any clear systematic concept on which the separation into three subfamilies is based. Not even the descriptions would allow one to attribute a genus to one of the subfamilies. The extensive use of conchological characters, many of which are known to be or should be suspected to be the result of convergent evolution, restricts the study to the level of knowledge of earlier contributions. Phrases like "is closely related" often have to be understood as "is most similar [conchologically]." The same applies to the recognition of the genera. The descriptions of the randomly selected Cuban genera *Blaesospira* Crosse, 1890 (p. 89) and *Guajaibona* Torre and Bartsch, 1941 (p. 91), for example, are identical to the word, except for the addition in the latter of "Whorls nearly adnate," a character that is not described for *Blaesospira*. No further remark is given. Another example: the genus *Parachondria* Dall, 1905 is said to be "similar to *Colobostylus* [which belongs to another subfamily] but usually has a higher spire, a non-sinuate lip, and rarely tufts" (p. 42). To add a last example and hereby provoke future research: I failed to find any argument for why breathing devices should have "inexplicably" evolved several times independently in all three subfamilies in Cuba and in a few annulariids in the Bahamas instead of questioning the reliability of the currently-applied system.

As to the general remarks on zoogeography, I am perhaps too curious to find clues to understand what really happened in the geological formation of the Caribbean region and the development of its flora and fauna to be satisfied with an account on biogeography and endemism that only tries to match the geologic evidence with the annulariid distribution. While this distribution pattern results from a systematic concept that constantly appears to have incorporated the geological evidence it remains simple story telling instead of searching for independent characters and patterns in the Annulariidae for reasoning and concluding.

Despite some drawbacks, the book will inevitably serve as a source for future workers on the subject and will certainly be helpful for students of local faunas as an excellent summary of all nomenclatural issues in Annulariidae. Real progress in understanding the phylogeny and evolution of the family in the Caribbean region has been made elsewhere (e.g., Thompson 1978) and will be greatly stimulated by Watters' contribution.

To end with Watters: "It is hoped that it will be the basis for detailed anatomical and genetic studies" (p. 1).

LITERATURE CITED

Rees, W. J. 1964. A review of breathing devices in land operculate snails. *Proceedings of the Malacological Society of London* **36**: 55-66, pls. 3-5.

Thompson, F. G. 1978. A new genus of operculate land snails from Hispaniola with comments on the status of family Annulariidae. *The Nautilus* **92**: 41-54.

Accepted: 21 December 2006

WCM
Antwerp, Belgium
15 - 20 July 2007

UM

Universiteit
Antwerpen

museum

WORLD CONGRESS OF MALACOLOGY
ANTWERP, BELGIUM, 15-20 JULY 2007

FIRST CIRCULAR: September 20th, 2006

The congress will be held on campus «Groenenborger» of the University of Antwerp. It is the 16th International Congress of UNITAS MALACOLOGICA (UM). The congress will also host the 73rd annual meeting of the AMERICAN MALACOLOGICAL SOCIETY (AMS). All payments will be in EUROS (€).

The congress is open for all contributions in the field of malacology and will host several exciting, open symposia, including:

- «Sexual selection» (organised by R. Chase & J. Koene)
- «Micromolluscs» (organised by D. Geiger)
- «Molluscs as models in evolutionary biology: From local speciation to global radiation» (organised by M. Glaubrecht & T. von Rintelen)
- «Molluscan models: Advancing our understanding of the eye» (organised by J. Serb & L. Robles)
- «Inventorying the molluscan fauna of the world: Frontiers and perspectives» (organised by P. Bouchet & S. Panha)
- «Neogastropod origins and evolution» (organised by J. Harasewych)

Yet, there is still room for further symposium or session proposals…

There will also be a contributed papers session and a poster session, with posters on display throughout the conference. The conference will start with an « icebreaker » on Sunday late afternoon, 15 July 2007. The scientific presentations are organised in four parallel sessions on Monday, Tuesday, Thursday and Friday. During the poster presentation on Tuesday evening there will be a reception with wine, typical Belgian degustations, cheese and of course… a selection of Belgian beers. On Thursday evening AMS will host its annual auction of molluscan books and paraphernalia (no specimens) to benefit its student programs. The conference dinner will be on Friday evening (several options are still being considered). Wednesday is a free day during which participants can discover the many historical and beautiful places in Antwerp. They can also join one of the suggested congress activities or do whatever they want, of course!

Convenient, though modest accommodation will be available at the university campus (about 200 single and 20 double rooms with lavabo, but toilets and showers are shared [even though cabines are individual of course]; prices: 20€/person or 27€/person per night ; breakfast included). Hotel accommodation will be provided in the city centre of Antwerp, near « Antwerpen Centraal » railway station, the main bus terminals and the shuttle bus from/to Brussels international airport. Prices range from 47.5€ (singles) to about 155€ (4 persons) per room per night (breakfast included).

ACCOMMODATION WILL BE PROVIDED ON A FIRST COME FIRST SERVED BASIS

Congress registration fees are in € (before/after 30 April 2007):

Full registration, UM-members	220/270
Full registration, non-UM-members	280/330
Student, UM-member	110/150
Student, non-UM-member	160/200

Fees include registration, abstract book, icebreaker, lunches, drinks and the wine/beer/degustation poster reception. The congress dinner is not included.

There will be several student awards for oral and poster presentations, including six awards presented by UM and the Constance Boone Award presented by AMS.

UM will provide Travel Grants. Applicants must be a member of UM or of an affiliated organisation. If not, a three-year UM membership will be deduced from the grant. The *maximum amount* of any Travel Grant will be 800 € for applicants from outside Europe and 400 € for residents in Europe. Application forms will be sent out with the next circular and will be available from the WCM 2007 website and the UM website (see below). They can also be requested when pre-registering (see below).

AMS will also be offering travel grants to its student members - please check the AMS website (see below) for information and application.

The congress website will soon be activated. In the meantime additional info can be obtained at :

wcm@naturalsciences.be

You can also PRE-REGISTER at this E-mail address, indicating:
(1) what kind of presentation(s) you would like to give (NOTE: each participant can only act as first author of ONE oral presentation and ONE poster presentation),
(2) which accommodation you prefer (campus vs hotel + how many persons/room),
(3) what type of registrant you are (UM member, student UM, student non-UM),
(4) whether you want to receive a Travel Grant application form,
(5) whether you need a congress « invitation » or « acceptance » letter (sometimes needed for certain grant applications)

Please provide your contact information. **Pre-registration IS NOT A FORMAL BOOKING; it simply implies that you will be put on the congress mailing list, so that you will automatically receive the next circulars (via E-mail, unless explicitly requested otherwise)**.

Useful websites:

Website of UNITAS MALACOLOGICA:
http://www.ucd.ie/zoology/unitas/

Website of the AMERICAN MALACOLOGICAL SOCIETY:
http://www.malacological.org

About Antwerp :
http://www.antwerpen.be/eCache/BEN/52.html
http://www.aviewoncities.com/antwerp.html
http://www.trabel.com/antwerp.htm

Website of the University of Antwerp (look for campus « Groenenborger »):
http://www.ua.ac.be/main.aspx?c=.ENGLISH&n=25878

Belgian railways :
http://www.b-rail.be/main/E/index.php

Note : There are good international train connections between Antwerp and several major cities outside Belgium. All train tickets can be purchased on-line using your credit card.

International bus connections to Antwerp (Europe only):
http://www.eurolines.com/

A route planner for if you come by car :
http://www.viamichelin.com/viamichelin/gbr/tpl/hme/MaHomePage.htm

Airports :
Antwerp airport : http://www.antwerpairport.be/en/index.html
Brussels airport : http://www.brusselsairport.be/index.cfm?lang=en
Charleroi airport : http://www.charleroi-airport.com/BSCA/siteEN.nsf/.Accueil?Readform

VLM Airlines, the Flemisch regional airline, offers daily flights from London, Liverpool, and Manchester to Antwerp Airport, where you can take the bus to « Antwerpen Centraal » railway station (10min; 1.50 €).
Website of VLM : http://www.flyvlm.com/emc.asp

Brussels (Zaventem) is the main international airport in Belgium (home of SN Brussels Airlines and VirginExpress), with a shuttle bus to the city centre of Antwerp (1 bus/hour; trip takes 45min; 8 €). You can also take the train in Brussels Airport and switch trains in « Brussel Noord » railway station (5 trains/hour; 60-80min; 6.70 €).
Website of SN Brussels Airlines: http://www.flysn.be/en%5Fbe/home/default.aspx
Website of VirginExpress : http://www.virgin-express.com/

Charleroi (Brussels South) airport is a major hub of Ryanair. From Charleroi you can reach « Antwerpen Centraal » railway station by direct train (2 trains/hour; 90-100min; 12.40 €).
Website of Ryanair : http://www.ryanair.com/site/EN/?culture=GB

Another convenient possibility is to fly to Amsterdam (Schiphol) and take the train from Schiphol Airport to Antwerp. You can take either the fast trains (Thalys; you have to book in advance and it is more expensive) or the « normal » direct trains (1train/hour; 120min; 26 €).

PLEASE NOTE THAT WE (= CONGRESS ORGANISATION) WILL NEITHER PROVIDE TRANSPORTATION, NOR WILL WE PICK UP PEOPLE AT AIRPORTS OR RAILWAY STATIONS. WE COUNT ON YOUR SCOUTING TALENTS!

Currency Converter :
http://www.oanda.com/convert/classic?user=onlineconversion&lang=en

SEE YOU IN ANTWERP !

Thierry Backeljau
President of Unitas Malacologica

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INFORMATION FOR CONTRIBUTORS

The *American Malacological Bulletin* is the scientific publication of the American Malacological Society and publishes notable contributions in malacological research. Manuscripts concerning any aspect of original, unpublished research, important short reports, and detailed reviews dealing with molluscs will be considered for publication.

Each original manuscript and accompanying illustrations must be submitted with two additional copies for review purposes. Text must be printed in 12 pt font on one side of 8-1/2 × 11 inch paper, double-spaced, with all pages numbered consecutively. Leave ample margins on all sides.

The form of the manuscript should follow that outlined in the *Council of Biology Editors Style Manual* (sixth edition, 1994). This can be purchased from the CBE, 11 S. LaSalle Street, Suite 1400, Chicago, IL 60603, USA.

Text should be arranged in sections as follows:

1. Cover page with title, authors, addresses, email addresses, and suggested running title of no more than 50 characters and spaces. Authors should also supply five key words, placed at the base of this page, for indexing purposes. Key words should not duplicate terms already in title.
2. Abstract (less than 5% of manuscript length)
3. Text of manuscript starting with a brief introduction followed by methodology, results, and discussion. Separate sections of text with centered subtitles in capital letters.
4. Acknowledgments
5. Literature cited
6. Figure legends
7. Tables (each on a separate sheet, headed by a brief legend)

All binomens, excluding non-molluscan taxa, must include the author and date attributed to the taxon the first time the name appears in the manuscript, such as *Crassostrea virginica* (Gmelin, 1791). The full generic name and specific epithet should be written out the first time a taxon is referred to in each paragraph. The generic name can be abbreviated in the remainder of the paragraph as follows: *C. virginica*.

References should be cited within text as follows: Hillis (1989) or (Hillis 1989). Dual authorship should be cited as follows: Yonge and Thompson (1976) or (Yonge and Thompson 1976). Multiple authors of a single article should be cited as follows: Beattie *et al.* (1980) or (Beattie *et al.* 1980).

In the section of literature cited, references should also be typed double-spaced. All authors must be fully identified and listed alphabetically; journal titles should not be abbreviated. Citations should be formatted as follows:

Donovan, D. A., J. P. Danko, and T. H. Carefoot. 1999. Functional significance of shell sculpture in gastropod molluscs: Test of a predator-deterrent hypothesis in *Ceratostoma foliatum* (Gmelin). *Journal of Experimental Marine Biology and Ecology* **236**: 235-251.

Seed, R. 1980. Shell growth and form in the Bivalvia. *In*: D. C. Rhoads and R. A. Lutz, eds., *Skeletal Growth of Aquatic Organisms*, Plenum Press, New York. Pp. 23-67.

Yonge, C. M. and T. E. Thompson. 1976. *Living Marine Molluscs*. William Collins Son and Co., Ltd., London.

Dall, W. H. 1889. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877-78) and in the Caribbean Sea (1879-80), by the United States Coast Survey Steamer "Blake," Lieutenant-Commander C. D. Sigsbee, U. S. N., and Commander J. R. Bartlett, U. S. N., commanding. Report on the Mollusca, Pt. 2: Gastropoda and Scaphopoda. *Bulletin of the Museum of Comparative Zoölogy* **18**: 1-492, pls. 10-40.

Orbigny, A, d'. 1835-46. *Voyage dans l'Amérique Méridionale (le Brésil, la République Orientale de l'Uruguay, la République Argentine, la Patagonie, la République du Chili, la République de Bolivia, la République du Pérou), exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833. Vol. 5, Part 3 (Mollusques)*. Bertrand, Paris. Dates of publication: pp. 1-48, [1835], pp. 49-184 [1836], pp. 185-376 [1837], pp. 377-408 [1840], pp. 409-488 [1841], pp. 489-758 + pls. 1-85 [1846].

Hurd, J. C. 1974. *Systematics and Zoogeography of the Unionacean Mollusks of the Coosa River Drainage of Alabama, Georgia and Tennessee.* Ph.D. Dissertation, Auburn University, Alabama.

U.S. Environmental Protection Agency. 1990. Forest riparian habitat survey. Available at: http://www.epa.gov/wateratlas/geo/ii16_usmap.html 25 January 2003.

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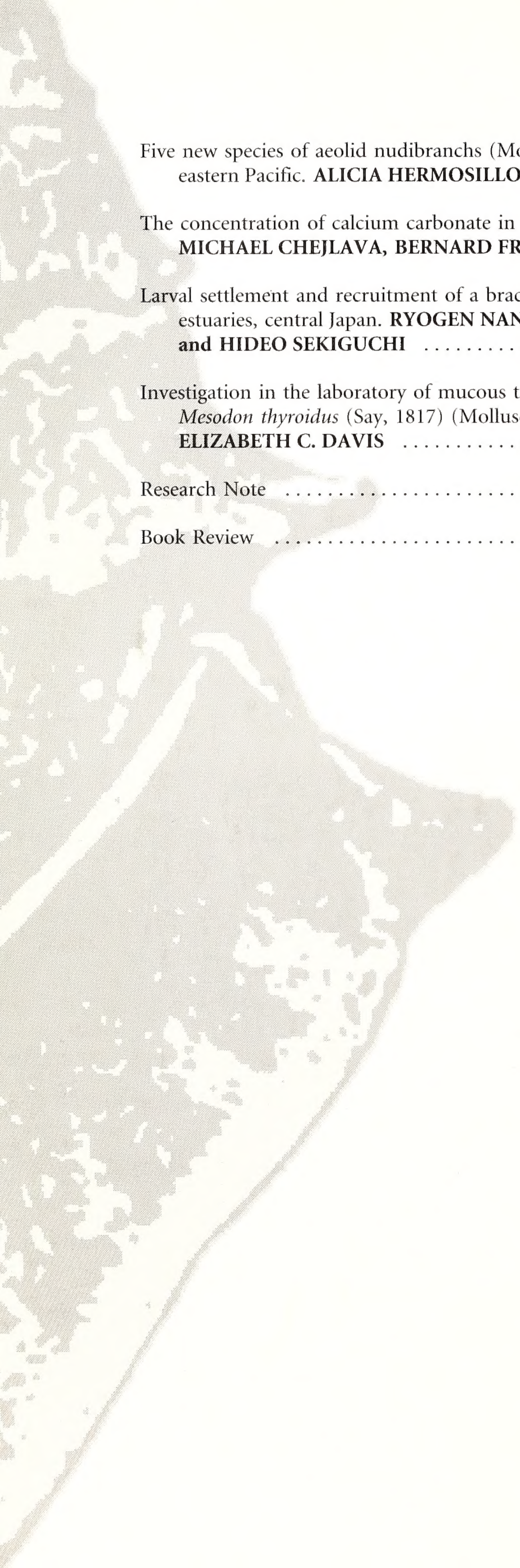

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